The persistence of *Sargassum* communities on coral reefs: resilience and herbivory

Thesis submitted by

Zoe Loffler *BSc (Hons)*

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James Cook University, Townsville, Queensland

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Dr. Andrew Hoey, Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland, Australia

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Abstract

Many of the world's ecosystems are in decline, with the combined effects of climate change and local anthropogenic stressors leading to shifts in the dominant habitat-forming organisms across a range of terrestrial and aquatic ecosystems. Such shifts not only represent a change in the structure and functioning of these ecosystems, but also the goods and services they provide. Within coral reef ecosystems, shifts from coral- to macroalgae-dominance are becoming increasingly common and, once established, macroalgae-dominated states are difficult to reverse. As such, understanding the capacity of herbivores to consume macroalgae, thereby preventing its establishment and reversing shifts to macroalgae-dominance is vital. However, the vast majority of research in this area has investigated the capacity of herbivores to remove macroalgal biomass without considering the longer term, ecological implications of the removal for macroalgal population dynamics. In this thesis, I seek to first understand how the ecology of a prevalent macroalga on degraded coral reefs, *Sargassum*, contributes to its resilience to disturbance, and then investigate herbivory of the *Sargassum* components (specifically, holdfasts and propagules) that are likely to be instrumental in promoting its persistence and spread on degraded and inshore coral reefs.

First, I examined the contrasting response of coral and macroalgae (Sargassaceae) communities to frequent disturbance using benthic monitoring data (2013-2017) from the Turtle Group, a series of inshore reefs in the northern Great Barrier Reef (GBR). Initially, five of the six monitored sites were either Sargassaceae or coral-dominated, while the sixth had a mixture of coral and macroalgae. Following three major disturbances in successive years (severe cyclones in 2014 and 2015, and a pan-tropical coral bleaching event in 2016), the ecosystem was essentially ‘reset’, as

coral and Sargassaceae cover at all sites decreased to between 0-5 % in 2014-2015. However, the Sargassaceae at these sites quickly recovered to over 70 % cover only 1-2 years after the disturbance. In contrast, coral communities did not show any evidence of recovery. Furthermore, at one previously coral-dominated site, the cover of Sargassaceae increased from 0 % to 28 % cover post-disturbance, indicating that Sargassaceae has the capacity to not only rapidly recover after disturbance, but also to rapidly colonise sites where it was previously absent. However, it is unknown if regrowth from holdfasts remaining on the benthos or growth from newly settled recruits enabled the rapid rate of recovery.

To investigate the potential contribution of holdfasts and propagules to the recovery of *Sargassum* populations post-disturbance, I experimentally simulated the physical removal of macroalgal biomass from *Sargassum* beds at Orpheus Island, an inshore coral reef on the GBR, and monitored recovery for 11 months. Trimming *Sargassum* biomass but leaving the holdfast intact had no detectable effect on the density, height or biomass of *Sargassum* compared to adjacent intact, or control, areas after five months. In contrast, in areas where holdfasts were also removed, holdfast density and thalli height only recovered to 78 and 66 % of control values, respectively, and *Sargassum* biomass only recovered to 50 % of control biomass after 11 months. Given the importance of holdfasts to the resilience of *Sargassum* beds, I also investigated the ability of herbivores to remove holdfasts. Exposing pieces of dead coral with attached *Sargassum* holdfasts to local herbivore assemblages resulted in a 70 % decline in the number of holdfasts over four months compared to those protected from herbivores. The resilience of *Sargassum* to disturbance through regrowth from holdfasts indicates that storms and cyclones are unlikely to result in sustained reductions in *Sargassum* biomass on coral reefs, however, the removal of *Sargassum*

holdfasts resulted in a significant decrease in the height and density of *Sargassum*, indicating that holdfasts must be removed in order to reduce *Sargassum* biomass.

In Chapter 4, I further explore the potential for herbivores to damage and/or remove holdfasts and investigate the capacity for *Sargassum* to regrow from damaged holdfasts. Underwater video cameras were used to investigate the susceptibility of *Sargassum* components (blades, stipes and holdfasts) to herbivory. Entire thalli of *Sargassum swartzii* were placed on the reef crest at Lizard Island in the northern GBR and monitored using photographs and video recordings for 24 days. The blades of the *S. swartzii* were rapidly removed (100 % in 2 days) by herbivores, whereas the stipes and holdfasts were less susceptible to herbivores. After 24 days, 72 % of experimental thalli had partial stipes remaining, and only one holdfast (out of 53) had been removed; all of the remaining holdfasts were largely undamaged. When *S. swartzii* holdfasts within natural stands were experimentally damaged (0, 25, 50, or 75 % removed), there was no detectable effect on thallus height or holdfast size among regrown thalli after one year. There was, however, a 50 % reduction in survival for *S. swartzii* individuals when 75 % of the holdfast was removed. This study demonstrated that holdfasts of *S. swartzii* are extremely resistant to herbivory, and that incidental bites on *S. swartzii* holdfasts are unlikely to affect their growth or survival unless three-quarters of the holdfast is removed.

Although the importance of herbivores in preventing shifts to macroalgae-dominance on coral reefs is well-established, the removal of macroalgal propagules within the Epilithic Algal Matrix (EAM: a conglomerate of short, productive turf algae, macroalgal propagules, detritus, microbes, and invertebrates) has largely been inferred rather than empirically demonstrated. To determine if the presence of *Sargassum swartzii* propagules in the EAM affected the feeding rate of grazing fishes, and if any

grazing affected the survival of *S. swartzii* propagules, I compared feeding on settlement tiles with EAM only, to those with *S. swartzii* propagules settled within the EAM. Paired settlement tiles (EAM only and EAM with propagules) were deployed on the reef crest and flat at Lizard Island in the northern GBR with video cameras for six days, with caged pairs to act as controls. While survival of *Sargassum* propagules was 39 % lower on tiles exposed to local fish assemblages than on caged tiles, grazing rates were 36 % lower on tiles that had *S. swartzii* propagules within the EAM than on tiles with EAM only. Surprisingly, these patterns were largely driven by small-bodied fishes from the genus *Ecsenius* (F. Blenniidae), which took significantly more bites on the tiles than any other fishes, and likely contributed to the decrease in propagule density on exposed tiles. These results suggest that smaller-bodied grazers may play a greater role in propagule removal than previously assumed, and that grazing fishes are able to detect the presence of *S. swartzii* propagules growing within the EAM and may prefer to graze areas free of propagules.

Finally, I investigate the importance of structurally complex microhabitats to the recruitment, growth and survival of *Sargassum swartzii* propagules. Fertile thalli of *S. swartzii* were induced to release spores and the spores allowed to settle onto terracotta settlement tiles that had a series of 3 mm deep crevices evenly spaced on their top (exposed) surface. Recruitment of *S. swartzii* within crevices was 21 % greater, but propagules were 18 % shorter, 18-days post-settlement than on adjacent exposed surfaces. Exposing tiles to local fish assemblages on the reef crest and flat at Lizard Island for five days showed that survival of propagules was 90 % greater in crevices than on exposed areas of the tiles on the reef crest, but not on the reef flat. Underwater video footage revealed that few fishes fed from within the crevices (18 % of all bites) with the majority of feeding being concentrated on the exposed surface of

tiles. Once again, small-bodied fishes from the family Blenniidae (predominantly *Ecsenius* spp.) accounted for the majority of the feeding activity on the tiles, and likely contributed to the mortality of propagules. Structurally complex microhabitats, such as crevices, may therefore be important for the proliferation of *Sargassum* on coral reefs through the provision of refugia from herbivory.

Overall, this thesis demonstrates the extraordinary resilience of *Sargassum* to disturbance. The capacity of *Sargassum* to recover after disturbance appears to be related to its ability to regenerate from holdfasts and may be further reinforced by the recruitment and growth of propagules. The persistence of *Sargassum* on coral reefs is likely enhanced by the reluctance of herbivores to consume holdfasts and the ability of *Sargassum* to regrow from holdfasts that have sustained significant damage. As a consequence, sustained browsing (preventing regrowth of the stipe and blades) may be more important in reversing macroalgae-dominance than physical removal of holdfasts by herbivorous fishes. Although small-bodied grazing fishes contributed to the mortality of *Sargassum* propagules, lower grazing rates on areas of the EAM containing propagules and within crevices may contribute to the survival of developing *Sargassum*, potentially enhancing the persistence of *Sargassum* beds on coral reefs. With predicted increases in the frequency and intensity of disturbances affecting coral reefs, the results of this thesis indicate that the ecology of *Sargassum* affords it a large capacity to withstand future disturbances, to the likely detriment of coral communities already under pressure from climate change.

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Chapter 1: General introduction

Ecosystems are shaped by interactions between organisms, environmental conditions and disturbances (Levin 1998, Scheffer et al. 2001). Climate-induced and local anthropogenic disturbances are increasingly becoming major drivers of ecosystem structure, and have led to shifts between alternate assemblages of species across a number of the world's ecosystems (Folke et al. 2004, Rocha et al. 2015). Such shifts represent a fundamental change in the structure and functioning of these ecosystems and are characterised by thresholds, feedbacks and hysteresis (Folke et al. 2004; Fig. 1.1). Shifts to new regimes have been reported in lakes, kelp forests, woodlands, deserts and on coral reefs (Scheffer et al. 2001). Once established, these 'new' regimes can be particularly difficult to reverse due to positive feedbacks among elements of the new assemblage that reinforce the regime (Scheffer and Carpenter 2003, Mumby and Steneck 2008). Regime shifts, and the associated fundamental changes in ecological structure and functioning, also affect ecosystem goods and services (Scheffer et al. 2001, Natalie et al. 2011, Crépin et al. 2012, Rocha et al. 2015). Identifying the mechanisms underpinning regime shifts is vital to predicting and reversing shifts to unwanted ecosystem states.

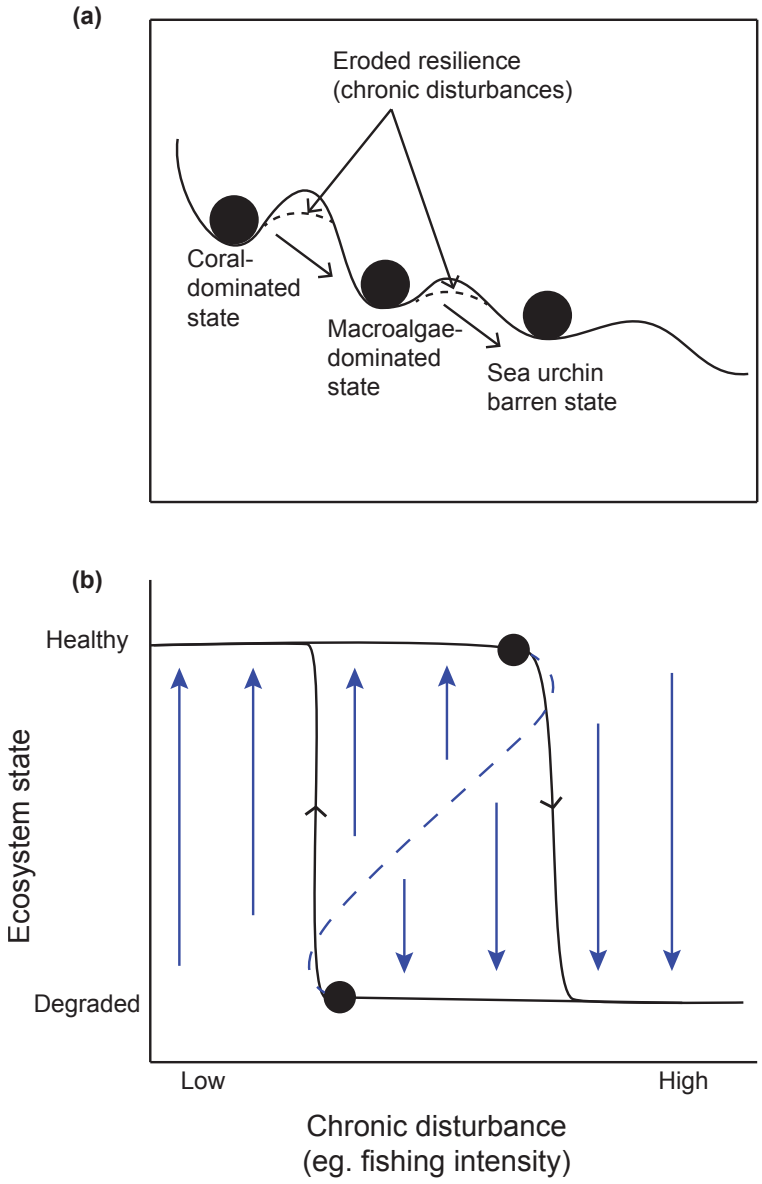

Figure 1.1: Conceptual model showing shifts between regimes in coral reef ecosystems. (a) Feedbacks maintain ecosystems in one state unless these feedbacks are eroded by chronic disturbances and/or an acute disturbance overcomes the feedbacks and displaces the ecosystem to a new ecosystem state, a 'regime shift'. (b) Schematic showing trajectories between healthy and degraded ecosystems with changing levels of a chronic disturbance; the path to recovery will follow a different trajectory than the path of initial decline due to positive feedbacks causing hysteresis. Disturbances can displace the systems away from their equilibrium, however, positive feedbacks (blue arrows) will quickly return the ecosystem to its previous state provided it does not cross the blue dashed line connecting the two tipping points. Adapted from Bellwood et al. (2004) and Hughes et al. (2010).

Both chronic (or press) and acute (or pulse) disturbances can act as drivers of change in ecosystems, particularly when acting in concert (Hughes 1994, Scheffer et al. 2001;

Fig. 1.1a). Chronic disturbances such as drought, eutrophication and overfishing undermine the resilience of an ecosystem, making it more susceptible to change from acute disturbances (Folke et al. 2004, Mumby et al. 2007). The resilience of an ecosystem refers to its ability to absorb and withstand shocks, retaining the same functions and feedbacks necessary to maintain the original ecosystem state (Holling 1973, Folke et al. 2004). In effect, acute disturbances push the system away from their equilibrium state (Fig. 1.1b). In resilient ecosystems, positive feedbacks quickly return the ecosystem to its original state, however, if the resilience of the system has been compromised, acute disturbances may push the system beyond the influence of positive feedbacks and into another basin of attraction, resulting in a reorganisation of the ecosystem and alteration of ecosystem functioning (Rocha et al. 2015; Fig. 1.1a). In recent decades, the frequency and severity of both chronic and acute disturbances has been increasing, resulting in widespread changes to the structure and functioning of many ecosystems, including coral reefs (Scheffer et al. 2001, Knutson et al. 2010, Hughes et al. 2018).

On coral reefs, a common shift from a desired to an undesired regime is the replacement of corals by fleshy macroalgae (Done 1992, Hughes 1994, Rasher et al. 2013, Graham et al. 2015). Such shifts have typically occurred when the resilience of coral-dominated ecosystems are compromised through the removal of herbivores by fishing, and the system is exposed to an acute disturbance (e.g., a severe storm or coral bleaching event) that causes widespread coral mortality (Done 1992, Hughes 1994, Graham et al. 2015). Once established, macroalgae-dominated regimes can be extremely difficult to reverse (Done 1992, Hughes 1994, Bellwood et al. 2004), as large fleshy macroalgae are only palatable to a select group of herbivores (Hoey and

Bellwood 2009), and a new set of feedbacks reinforce the macroalgal presence (Mumby and Steneck 2008, Wilson et al. 2012, Webster et al. 2015, Dell et al. 2016).

The role of herbivores in shaping algal communities on reefs has long been recognised (Hay 1981, Lewis 1986), however, the increasing incidence of shifts to macroalgal-dominated regimes has highlighted the critical importance of this group to the functioning and resilience of reefs (Hughes 1994, Bellwood et al. 2004, Cheal et al. 2010, Graham et al. 2015). This has led to a renewed focus on the role of individual herbivore species in ecosystem processes, distinguishing between those fishes that may have the capacity to either prevent (i.e., grazers) or potentially reverse (i.e., browsers) coral to macroalgae regime shifts (Bellwood et al. 2006a, Hoey and Bellwood 2009). The functional role and importance of different herbivorous species depends on the way they feed and the algal species they target (Bellwood et al. 2004, Bellwood et al. 2006a, Rasher et al. 2013, Graham et al. 2015).

Grazing fishes target components of the Epilithic Algal Matrix (EAM), a conglomerate of short turf algae, macroalgae propagules, microbes and detritus (Wilson et al. 2003), and are thought to remove small macroalgal propagules within the EAM during their foraging, preventing the establishment of macroalgal populations. This is supported by inferences from studies that have documented the rapid proliferation of macroalgae in areas where these herbivores are excluded (Lewis 1986, Hughes et al. 2007). However, the contribution of grazing fishes to propagule removal has never been empirically investigated (but see Diaz-Pulido and McCook (2003)), and the grazing fishes responsible for removing macroalgal propagules have not been identified. In contrast, studies have identified the browsing fishes that target large, fleshy macroalgae (Hoey and Bellwood 2009, Vergés et al. 2011, Rasher et al. 2013), seen as being instrumental to reversing macroalgae-dominated regimes (Bellwood et al.

2006a). Despite this large body of research investigating the contribution of herbivores (particularly browsers) to reversing macroalgal-dominated regimes, the vast majority of studies have focused on the consumption of algal biomass without considering other mechanisms that could also reduce macroalgal biomass and facilitate a return to coral dominance.

Most studies investigating the reversal of macroalgae-dominated regimes have reported rates of herbivory without considering other mechanisms, such as disturbance, that may reduce macroalgal biomass on degraded coral reefs and facilitate reef recovery (Mantyka and Bellwood 2007a, Hoey and Bellwood 2009, 2010a, Vergés et al. 2011, Loffler et al. 2015). However, disturbance events such as storms and cyclones can remove large amounts of macroalgae from a reef in a single event, essentially 'resetting the system' (De Ruyter van Steveninck and Breeman 1987, Lapointe et al. 2006). Previous research has suggested that storms may offer a window of opportunity for the recovery of coral populations through the large-scale removal of macroalgae (Graham et al. 2013). However, the window for the replenishment of coral populations will largely depend on the resilience of both coral and macroalgae to these disturbance events. It is currently not well understood how storm events affect macroalgae biomass on macroalgae-dominated coral reefs.

The proliferation of many macroalgal species on degraded coral reefs may be due to their fast growth, perennial nature (i.e., ability to regrow from holdfasts; Ang Jr 1985, Martin-Smith 1993, Vuki and Price 1994), and extensive release of fast-growing spores during reproduction (Vadas et al. 1992). *Sargassum*, a tall, brown, fleshy macroalgae that is common on degraded and inshore coral reefs (Rasher et al. 2013, Chong-Seng et al. 2014), typifies this perennial regrowth, high reproductive output life-history (Martin-Smith 1993). These traits may contribute to *Sargassum*'s dominance of

the benthic assemblage on numerous degraded and inshore coral reefs worldwide (Ang Jr 1985, Done 1992, Hoey et al. 2011, Chong-Seng et al. 2012, Rasher et al. 2013, Dell et al. 2016) and may promote high resilience to disturbance (Sousa 1980). However, despite the likely importance of these traits to the proliferation and stability of *Sargassum* communities on coral reefs (Engelen et al. 2005), previous studies investigating herbivory of *Sargassum* have largely not considered how its ecology may critically interact with herbivory to facilitate its persistence (Mantyka and Bellwood 2007a, Hoey and Bellwood 2010b, Loffler et al. 2015).

1.1 Aims and thesis outline

Given our poor understanding of how herbivory and disturbance can structure benthic communities on degraded coral reefs, the main objective of this thesis was to investigate how the ecology of *Sargassum* contributes to its persistence and potential expansion on inshore coral reefs of the Great Barrier Reef. Specifically, the primary aims of this thesis were to: (1) compare the resilience of coral and *Sargassum*-dominated communities on inshore coral reefs to multiple severe disturbances, (2) investigate the resistance and resilience of *Sargassum* holdfasts to disturbance and herbivory, and the relative contribution of holdfasts vs. new recruits in the replenishment of *Sargassum* assemblages, (3) identify which fishes remove *Sargassum* propagules from within in the Epilithic Algal Matrix and how the presence of propagules affects feeding by grazing fishes and (4) investigate how small crevices affect the recruitment, growth, and survival of *Sargassum* propagules.

These aims are addressed in the following six chapters. **Chapter 2** examines the responses of both coral- and macroalgal-dominated assemblages to multiple severe disturbances (two cyclones and two thermal bleaching events) on a group of inshore

coral reefs. **Chapter 3** builds on this foundation and experimentally simulates the effects of a severe storm on *Sargassum* assemblages *in situ* to assesses the relative importance of regrowth from holdfasts versus the settlement of new propagules in the recovery of *Sargassum* biomass over an 11-month period and assesses the susceptibility of holdfasts to herbivory. **Chapter 4** further explores the findings of Chapter 3, using stationary underwater video cameras and experimental manipulation to investigate the resistance and resilience of *Sargassum* thalli, particularly holdfasts, to herbivory and physical damage. **Chapter 5** examines rates of herbivory on surfaces with and without early post-settlement *Sargassum* propagules, to determine if the presence of *Sargassum* propagules within the EAM dissuades feeding by grazing fishes. **Chapter 6** further investigates herbivory and survival of *Sargassum* propagules, examining how small crevices affect the settlement, growth and herbivory of early post-settlement propagules. Finally, **Chapter 7** (General Discussion) summarises my findings, considers the implications and significance of these findings to the field of ecology, and identifies further research questions arising from this thesis.

Chapter 2: Contrasting recovery of coral and *Sargassum* communities on a highly disturbed inshore coral reef[1]

2.1 Introduction

Many of the world's ecosystems are in decline (Malhi et al. 2008, Wernberg et al. 2016, Hughes et al. 2018), with regime shifts between alternate assemblages of species becoming increasingly common (Scheffer et al. 2001). These shifts represent a large and often unidirectional change in the structure and functioning of these systems, as established shifts can be difficult to reverse (Scheffer and Carpenter 2003, Folke et al. 2004). The stability, or resilience, of these different regimes is believed to arise from interactions among elements of each regime that form positive feedbacks, reinforcing and maintaining the regime (Mumby and Steneck 2008, Scheffer et al. 2009, Hughes et al. 2010). While models predict that positive feedbacks and the resilience they provide may be eroded by chronic stressors, rendering the system more susceptible to change following acute disturbances, there have been few empirical investigations into the response of different regimes to disturbance.

Coral reefs are one of the world's most biodiverse ecosystems, yet they are also one of the most threatened (Hughes et al. 2017a). The combined effects of climate change and local anthropogenic stressors have led to regional declines in the cover of live coral over recent decades (Connell et al. 1997, Hughes et al. 2003, De'ath et al. 2012, Hughes et al. 2018), with some reefs shifting from coral dominated systems to ones dominated by large fleshy macroalgae (Hughes 1994, Graham et al. 2006, Cheal et

[1] Hoey, A.S., Loffler, Z. Contrasting recovery of coral and *Sargassum* communities on a highly disturbed inshore coral reef. In prep.

al. 2010, Rasher et al. 2013). Such shifts have been widely attributed to chronic stressors, namely the removal of herbivores through fishing and/or eutrophication from land-based activities, yet they are commonly triggered by acute disturbances (e.g., thermal coral bleaching events, cyclones) that cause widespread coral mortality (Hughes 1994, Graham et al. 2015). These acute disturbances break the positive feedbacks and push the system toward a new basin of attraction (Rocha et al. 2015, van de Leemput et al. 2016). Once established, macroalgal-dominated regimes are difficult to reverse as they are reinforced by a suite of unique feedbacks that promote algal growth and inhibit the recovery of coral populations (Hoey and Bellwood 2011, Webster et al. 2015, Dell et al. 2016).

In coral reef ecosystems, acute disturbances such as severe storms and marine heat waves are generally considered in light of their effects on coral populations and the potential to shift the system toward macroalgal dominance, yet are rarely considered in terms of their capacity to initiate a shift from a macroalgal-dominated community back toward a more desired state of high coral cover (Graham et al. 2013). Indeed, increased water movement due to severe storms can dislodge individual macroalgal thalli, leading to large reductions in algal biomass (De Ruyter van Steveninck and Breeman 1987, Rogers 1997, Lapointe et al. 2006). Further, marine heat waves have been shown to cause high mortality of temperate phaeophytes (Wernberg et al. 2016), and could equally cause mortality of tropical macroalgae if their thermal maxima are exceeded during the event. Such large-scale mortality of macroalgae could release remaining corals from many of the detrimental effects of associating with the macroalgae (Tanner 1995, Box and Mumby 2007, Rasher and Hay 2014), provide bare substratum for the settlement of other benthic taxa (including corals), and thereby provide a 'window of opportunity' for the recovery of coral populations (Graham et al. 2013). The aim of this

study, therefore, was to investigate the responses of both macroalgae- (predominately *Sargassum* spp.) and coral-dominated assemblages to multiple severe disturbances on inshore reefs on the Great Barrier Reef. Specifically, annual surveys were used to examine how alternate benthic communities (i.e. coral-dominated and macroalgae-dominated) respond to severe disturbance events on an inshore coral reef.

2.2 Materials and Methods

2.2.1 Study sites

This study was conducted in the Turtle Group (14°43'S, 145°12'E), a group of inshore reefs located in the northern Great Barrier Reef (GBR), approximately 11 km from the Australian mainland coast. The mainland adjacent to the Turtle Group is characterised by minimal agricultural development, low cattle grazing and low human population density; nutrient input from these sources is minimal (Brodie et al. 2007). The reefs in the Turtle Group have been protected from all fishing activities since 2004 (McCook et al. 2010). Five sites were selected within the Turtle Group in 2013 and surveyed annually for five years (November 2013 - November 2017). Three sites were initially characterised by a high cover (56 to 77 % cover in 2013) of Sargassaecae (primarily *Sargassum swartzii* and *Sargassum cristaefolium,* and also *Cystoseira, Hormophysa, Sargassopsis* and *Turbinaria*) but had low coral cover (<10 %). Two sites had relatively high coral cover (averaging 35 % cover in 2013) and low cover of Sargassaecae (<1 % cover).

The Turtle Group was impacted by four major disturbances between 2013-2017. Cyclone Ita (category 4) crossed directly over the Turtle Group from the north east to south west on the 12th of April 2014, and Cyclone Nathan (category 3) passed from east to west across the Turtle Group on the 20th of March 2015 (Gordon et al. 2018). In

2016 and 2017, record sea surface temperatures triggered two pan-tropical mass coral bleaching events. On the GBR, the most severe heat stress occurred in the northern 1000 km section, which encompasses the Turtle Group, with 16 DHW (degree heating weeks) recorded, and sea surface temperatures averaging ~30°C in March during the 2016 bleaching event (Hughes et al. 2017b).

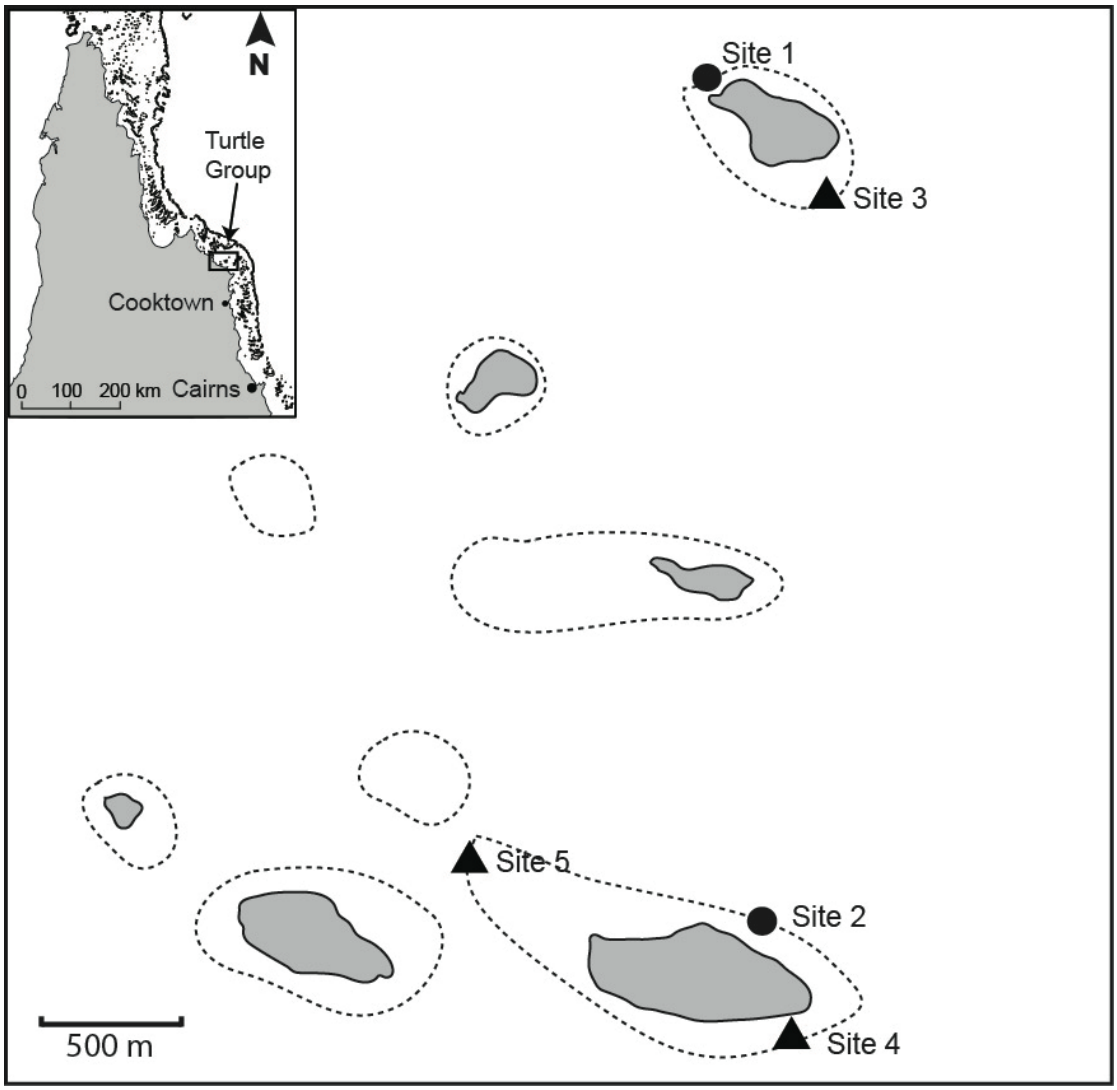

Figure 2.1: Map of surveyed sites between 2013-2017 within the Turtle Group Islands in the northern Great Barrier Reef, Australia. Insert shows position of the Turtle Group relative to the Australian mainland. The Turtle Group islands are approximately 11 km east of the mainland. Circles (sites 1 and 2) denote sites initially dominated by coral and triangles (sites 3-5) denote sites initially dominated by Sargassaceae.

2.2.2 Benthic surveys

Surveys to characterise the benthic assemblage in the Turtle Group were conducted at the five sites between October – November each year from 2013-2017 inclusive. At each site, four 50 m point intercept transects were used to quantify the benthic composition at one metre intervals along the transect. Transects were lain parallel to the reef crest at a depth of ~3 m, with a minimum of 5 m between adjacent transects. The substratum directly under the transect tape was recorded at 1 m intervals. Corals and macroalgae were identified to genus, with categories also included for sand, rubble, reef pavement, dead coral, sponges, ascidians, clams and zoanthids.

2.2.3 Statistical analysis

Two interactive Bayesian generalised linear models with a negative binomial error distribution (log link function) were used to analyse changes in (a) coral and (b) Sargassaceae among sites and years in response to disturbance. Count was included as the response variable, with year and site included as fixed factors. The models used weakly informative priors on intercept (normal(0,5)) and slope (normal(0,5)) coefficients and error standard deviation (Cauchy(0,4)). 4000 iterations, a warmup of 2000, three chains and a thinning factor of three were specified. Diagnostic plots were inspected to examine model fit. Planned contrasts examining coral and Sargassaecae cover between years 2013 and 2017 were also performed for each site. Analyses were conducted in R version 3.3.2.

Non-metric multi-dimensional scaling (nMDS) was used to examine changes in the benthic community composition at each site through time. Data were fourth-root

transformed and the analysis was based on a Bray-Curtis dissimilarity resemblance matrix, which does not consider joint absences to imply similarity among sites. nMDS analysis was performed using PRIMER version 6.

2.3 Results

In 2013, before the impact of Cyclones Ita and Nathan, coral cover was relatively high, averaging 38 ± 12 % across the two coral-dominated sites (Fig. 2.2a). However, after the cyclones, coral cover significantly decreased at both sites, to 3 ± 3 % in 2015 (Fig. 2.2a), and has remained low for the two years following (4 ± 1 % and 2 ± 3 % in 2016 and 2017, respectively). Overall, there was a significant decrease in coral cover at all sites between 2013 and 2017 (Fig. 2.3a). See Appendix A for model outputs.

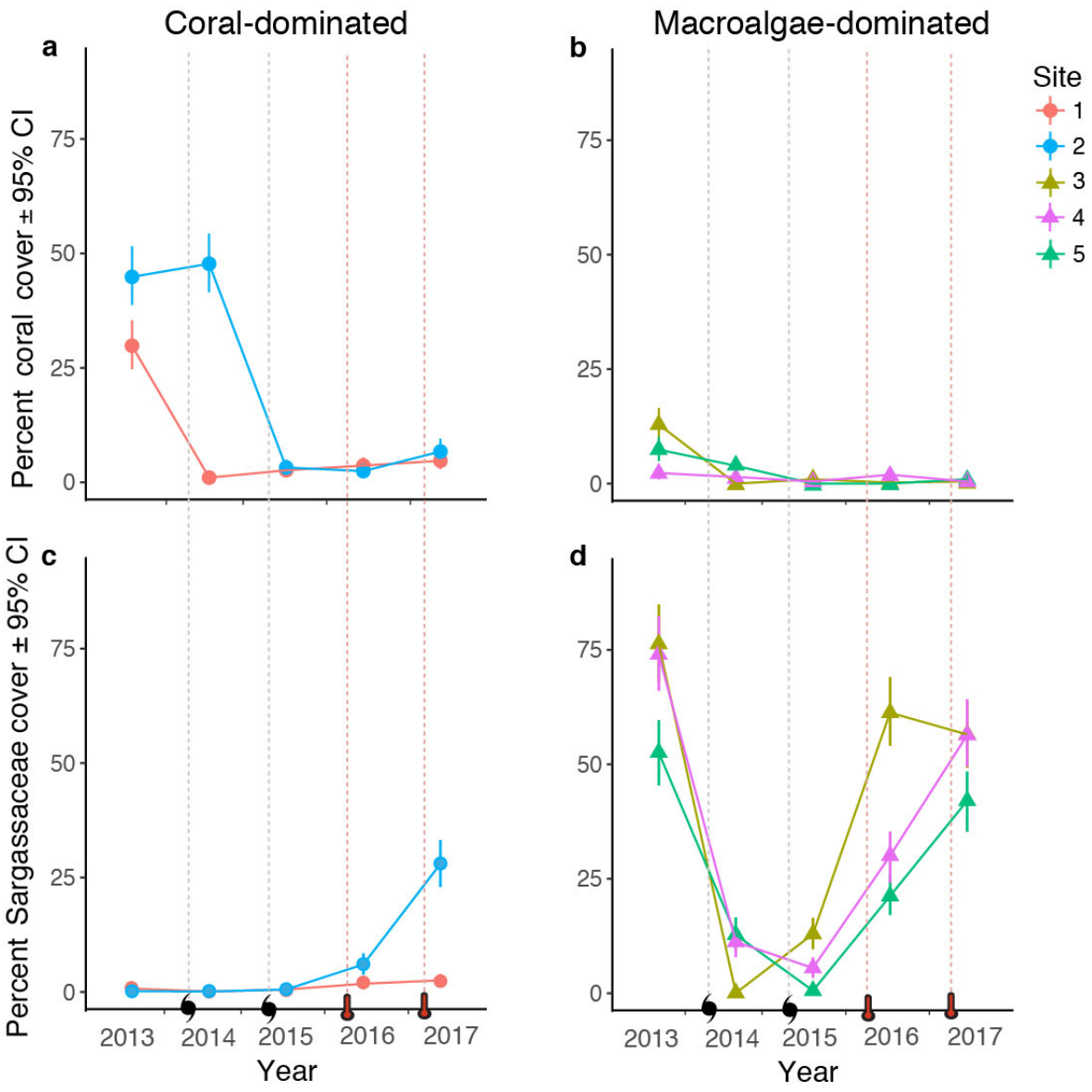

Figure 2.2: Percent cover of live scleractinian coral (a, b) and Sargassaceae (c, d) from 2013-2017 at five sites in the Turtle Group islands. Changes in the cover of live corals and macroalgae are presented separately for initially coral dominated sites (a, c) and initially macroalgal-dominated (i.e., Sargassaceae) sites (b, d). The approximate timing of the two cyclones and thermal bleaching events are shown on the x-axis. Individual points represent model estimates of the mean ± 95% Credible Intervals.

In 2013, cover of Sargassaceae was high at macroalgae-dominated sites (56 to 77 % cover; Fig. 2.2d), rapidly decreasing after Cyclone Ita, to between 0 and 11 ± 13 % cover across all sites in 2014, remaining low in 2015 after Cyclone Nathan. The cover of Sargassaceae rapidly increased between 2015 and 2016, with cover of Sargassaceae

recovering to within 15-20 % of pre-disturbance (i.e., 2013) levels. Interestingly, at one of the initially coral-dominated sites (site 2; coral cover in 2013 = 45 ± 14 %; Sargassaceae = 0 ± 0 %) the cover of Sargassaceae rapidly increased after cyclone Ita (from 1 ± 1 % in 2015, to 28 ± 6 % in 2017). Planned contrasts comparing Sargassaceae cover in 2013 with cover in 2017 showed that although regrowth was rapid, cover was still lower than pre-disturbance (i.e., 2013) levels at all initially macroalgae-dominated sites and had increased significantly at the two initially coral-dominated sites (Fig. 2.3b).

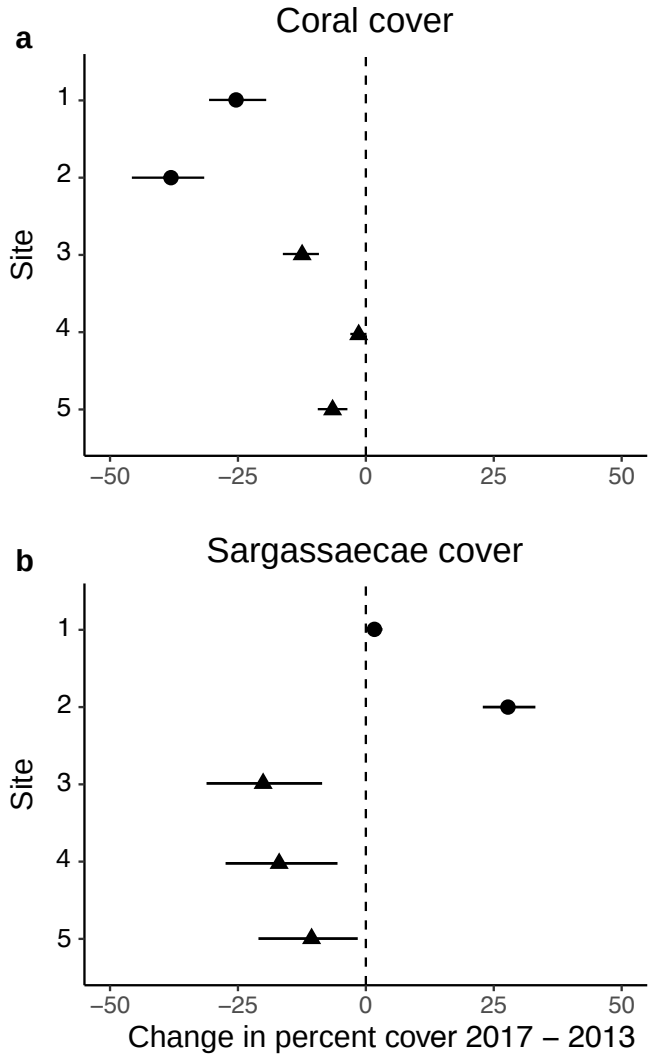

Figure 2.3: Planned contrasts comparing change in percent cover of coral (a) and Sargassaceae (b) at initially coral dominated sites (circles) and macroalgae dominated sites (triangles) between years 2013 and 2017. Estimates to the left of the dotted line indicate that cover was lower in 2017 than 2013 and estimates to the right indicate that cover was higher in 2017 than in 2013. Lines indicate 95 % higher posterior density intervals.

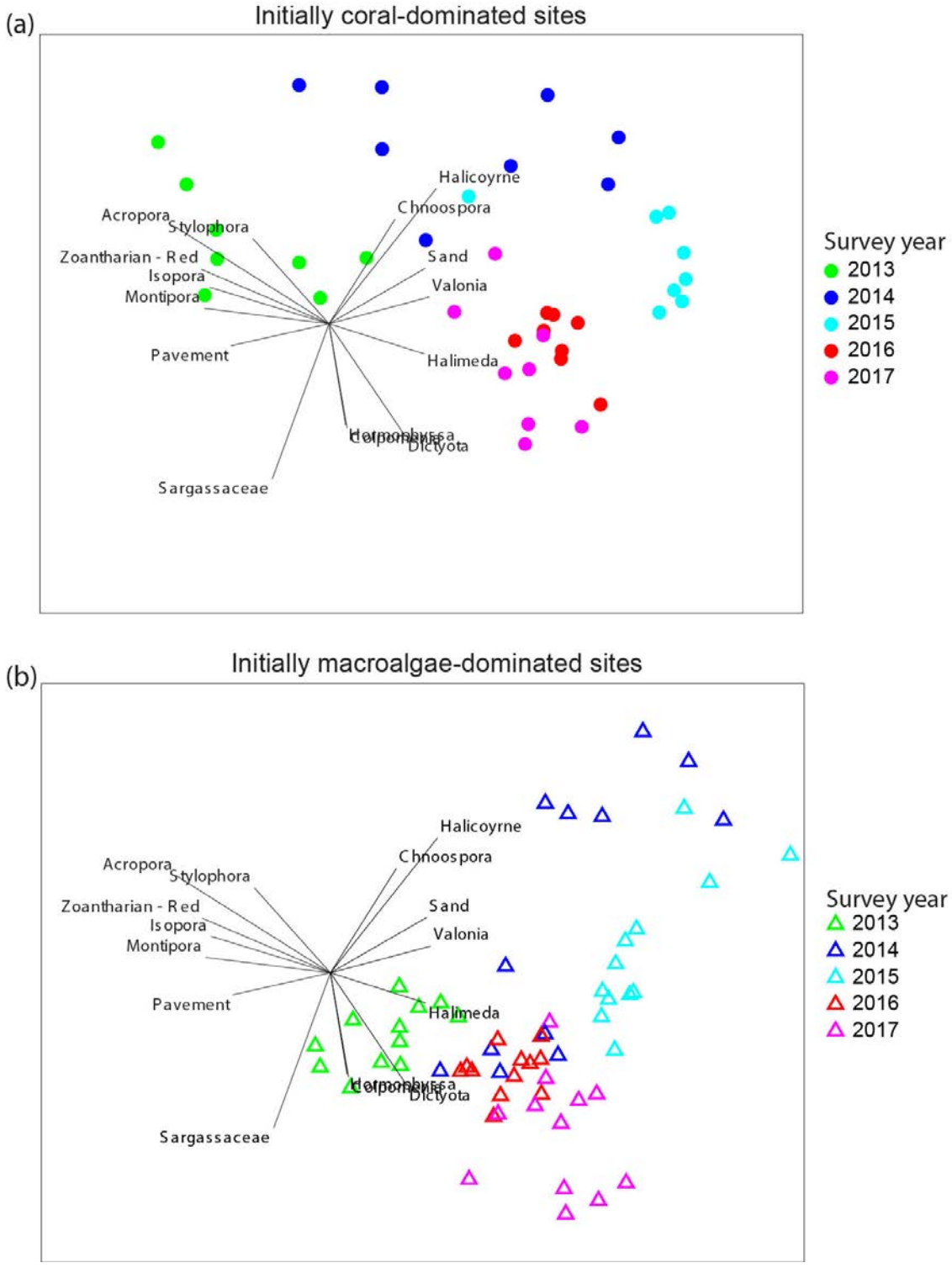

Figure 2.4: nMDS analysis showing the relationship between benthic assemblages from 2013-2017 across five sites in the Turtle Group Islands in the northern GBR. (a) benthic composition through time at initially coral-dominated sites (sites 1 and 2), (b) benthic composition through time at initially Sargassaceae-dominated sites (sites 3-5). Circles and triangles of the same colour indicate the surveys were performed in the same year. Each site/year combination includes four transects composed of 62 benthic categories. Only vectors with an R2 value greater than 0.4 are shown, for clarity.

The nMDS showed clear variation in benthic composition through time (Fig. 2.4). Years 2014 and 2015 show a dramatic shift in community composition compared to 2013, with low cover of both coral and Sargassaceae, and a high cover of the green alga *Halicoyrne* spp. at a number of sites, particularly those that were initially Sargassaceae-dominated (Fig. 2.4b). Years 2016 and 2017 show a return to dominance of Sargassaceae and other macroalgae across most sites (Fig. 2.4b), but do not show evidence of any increase in coral cover across sites, rather, coral-dominated sites trend toward macroalgal dominance (Fig. 2.4a).

2.4 Discussion

The response of an ecosystem to disturbance will largely be determined by the capacity of the dominant taxa structuring the ecosystem to resist change and/or recover following the disturbance (Connell 1978, Sousa 1980, Connell et al. 1997). In the present study, I found that both coral and Sargassaceae-dominated communities were highly vulnerable to multiple severe disturbances, with live corals and Sargassaceae showing marked declines following disturbance. These communities, however, showed contrasting post-disturbance recovery. Sargassaceae-dominated sites recovered to within 15 % of their original cover 1-2 years post-disturbance, whereas coral communities showed little evidence of recovery. Furthermore, the abundance of Sargassaceae at one of the previously coral-dominated sites increased from 0 to 28 % cover two years after the second cyclone, indicating that Sargassaceae also has the capacity to rapidly colonise new areas after disturbance. The findings of the present study suggest that the differing ecology and life history of coral and Sargassaecae provide contrasting capacities to recover following disturbance events.

Many macroalgae, and in particular those of the Sargassaceae, have life histories that may afford them the capacity to rapidly recover from disturbance events and the ability to colonise new areas (Vuki and Price 1994, Engelen et al. 2005). For example, *Sargassum* has a perennial cycle of spring/summer growth, reproduction, senescence to a holdfast base in winter, followed by rapid regrowth from the holdfast in spring (Ang Jr 1985, Martin-Smith 1993). This capacity to regrow from the holdfast may be critical in the re-establishment of populations following severe storms that can break *Sargassum* individuals at the flexible stipe, often leaving holdfasts intact on the benthos (Dayton et al. 1984, De Ruyter van Steveninck and Breeman 1987, Vuki and Price 1994). The recovery of Sargassaceae within 1-2 years of disturbance in the present study may have largely been facilitated by this innate capacity for regrowth from the holdfast. Indeed, studies in Puerto Rico and Curaçao have also reported the rapid recovery of shallow-water *Sargassum* communities to pre-disturbance levels only one year after cyclone disturbances (Category 5 Cyclones Allen and David in Puerto Rico (1979-1980); Category 4 Cyclone Lenny in Curacao (1999)) and cite regeneration from holdfasts and recruitment of new individuals as critical life history traits that provide *Sargassum* the ability to persist in areas subjected to large disturbance events (Ballantine 1984, Engelen et al. 2005). While regrowth from holdfasts may explain the recovery of Sargassaceae cover at the three macroalgae-dominated sites, the rapid increase in Sargassaceae at the previously coral-dominated sites is likely due to the dispersal and establishment of propagules (Deysher and Norton 1981, Engelen et al. 2005).

Corals, unlike macroalgae, are unable to quickly recover from disturbances, with recovery over 5-10 years rather than the 1-2 for Sargassaceae (Adjeroud et al. 2009, Linares et al. 2011, Gilmour et al. 2013). Severe cyclones can cause the complete

destruction of most coral colonies in an area, leaving behind fragments vulnerable to disease and burial amongst unconsolidated substrata and rubble (Harmelin-Vivien 1994, Fabricius et al. 2008), and the fecundity of surviving colonies is typically severely compromised (Lirman 2000, Baird et al. 2018). In addition, the widespread 2016 bleaching event that caused mortality of over 60 % of corals in the northern 700 km of the GBR (Hughes et al. 2017b), would have severely reduced the number of larvae produced in the November 2016 mass-spawning event, and, therefore, the number of larvae reaching the Turtle Group reefs. Worryingly, the increase in abundance of Sargassaceae at Site 2, a site previously dominated by corals, may also inhibit future coral recovery in this location, as settlement and survival of coral larvae can be reduced by already established macroalgae (Hughes et al. 2007, Birrell et al. 2008b, Diaz-Pulido et al. 2010, Dixson et al. 2014, Johns et al. 2018). The long-term recovery of corals at these reefs may be inhibited due to both the frequency and intensity of the disturbances (Yadav et al. 2018), and the proliferation of Sargassaceae and other macroalgae at previously coral-dominated sites (Adjeroud et al. 2009).

While most shifts to macroalgal-dominance have been associated with reductions in herbivores due to fishing and/or eutrophication from land-based run-off, the Turtle Group is largely isolated from anthropogenic nutrient inputs (Brodie et al. 2007) and has been protected from fishing since 2004 (McCook et al. 2010). Previous research has suggested that herbivores such as parrotfishes can increase their grazing rate in response to an increase in algal production post-cyclone, preventing shifts to fleshy macroalgae (Russ and McCook 1999). Further, McCook (1997) proposed that on the GBR, *Sargassum* may not be able to colonise new areas whilst herbivory remains high, however, 'natural' populations of herbivores appear incapable of preventing the recovery and expansion of macroalgae on these reefs. Despite the lack of chronic

stressors that are common to many macroalgae-dominated reefs (Hughes and Connell 1999), macroalgae rapidly recovered and proliferated on these reefs. The free space created on the benthos may have resulted in a rate of algal production that exceeded the capacity of herbivores to consume it (Hatcher and Larkum 1983), allowing many of the macroalgal propagules settling within the Epilithic Algal Matrix (EAM; a conglomerate of short, productive algal turfs, macroalgal propagules, detritus and microbes) to be released from top-down control and reach a size refuge from grazing fishes (Mumby 2006, Roff et al. 2015).

Marine heatwaves have caused significant mortality of temperate macroalgae (Wernberg et al. 2016) and have been hypothesised to have similar effects on tropical macroalgae (Fulton et al. 2019), however, there has been little to no research investigating the thermal tolerance of tropical *Sargassum*. The cover of Sargassaceae did not decrease in response to the 2016 and 2017 thermal anomalies, suggesting that the thermal limits of *Sargassum* were not exceeded during the events as they were for most corals in the region (Hughes et al. 2017b). With climate change causing increases in mean sea surface temperatures and increasing the frequency of bleaching events (Heron et al. 2016, Hughes et al. 2018), it is likely that *Sargassum* will be better able to survive these extreme heat events than corals.

This study provides substantial evidence of the resilience of Sargassaceae communities to frequent disturbance, and the potential for Sargassaceae to rapidly proliferate into areas previously dominated by corals. With disturbance frequency and severity predicted to increase with climate change (Hoegh-Guldberg et al. 2007), understanding the response of both coral and Sargassaceae to disturbance is becoming increasingly important in predicting how coral reef communities will change into the future. Further research investigating the mechanisms underpinning the resilience of

Sargassum to disturbance will help to clarify why *Sargassum* was able to both recover and increase its range so rapidly post-disturbance.

Chapter 3: Canopy-forming macroalgal beds (*Sargassum*) on coral reefs are resilient to physical disturbance[2]

3.1 Introduction

Many of the world's ecosystems are in decline (Vitousek et al. 1997, Malhi et al. 2008, Wernberg et al. 2016, Hughes et al. 2017b). The combined effects of climate change and local anthropogenic stressors have led to shifts in the dominant habitat-forming organisms across a range of terrestrial and aquatic ecosystems (Scheffer et al. 2001). Such 'regime shifts' are often triggered by an acute disturbance when a community is already under pressure from one or more chronic stressors (Sousa 1984, Ebeling et al. 1985, Scheffer et al. 2001, Folke et al. 2004). For example, extreme rainfall events associated with the El Niño Southern Oscillation, in conjunction with decreased grazing pressure, initiated a shift from an arid regime to a wooded regime in a temperate woodland ecosystem (Holmgren and Scheffer 2001). Similarly, on coral reefs, the removal of herbivores through overfishing and/or disease, coupled with disturbances that cause large-scale coral mortality (e.g., coral bleaching, hurricanes) can shift the ecosystem from a 'healthy' coral-dominated regime, to a less desired macroalgae-dominated regime (Hughes 1994).

Shifts in the dominant habitat-forming organism in an ecosystem following an acute disturbance, together with the relative stability of the new state and difficulties in reversing such states, has led to development of conceptual models describing the existence of alternate stable states (May 1977, Scheffer et al. 2001, Knowlton 2004).

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Such models are characterised by tipping points, feedbacks, hysteresis and the presence of multiple ecosystem states for a single set of environmental conditions (e.g., Scheffer et al. 2001, Mumby, Hastings & Edwards 2007). Although the concept of alternate stable states is appealing and widely accepted, there is a lack of empirical evidence supporting the existence of alternate states or hysteresis in most ecosystems (Connell and Sousa 1983, Dudgeon et al. 2010). Within coral reef ecosystems, numerous studies have identified positive feedbacks that reinforce the ecosystem state (typically a coral- or macroalgal-dominated state; reviewed in Mumby & Steneck 2008; van de Leemput et al. 2016). While the presence of positive feedbacks may explain a non-linear response of ecosystem state to changing environmental conditions and contribute to the resilience of that state, they are not in themselves evidence of alternate states. Therefore, in the context of this thesis, I consider coral- and macroalgal-dominated 'states' to be different regimes rather than alternate stable states.

Coral reefs are one of the world's most biodiverse and productive ecosystems, yet they are also one of the most threatened (Gardner et al. 2003, De'ath et al. 2012). The combined effects of global climate change and local disturbances (e.g., sedimentation, eutrophication, cyclones and crown-of-thorns starfish outbreaks) have led to regional declines in the cover of live corals (Hughes 1994, Bruno and Selig 2007, De'ath et al. 2012, Hughes et al. 2017b). When these disturbances are coupled with a reduction in herbivores, algal production may exceed consumption, resulting in a regime shift to a macroalgal-dominated community (Done 1992, Hughes 1994). Once established, macroalgae reduce the settlement, survival, growth and reproduction of corals (Kuffner et al. 2006, Box and Mumby 2007, Rasher and Hay 2010) and suppress the feeding of herbivores (Hoey and Bellwood 2011). These positive feedbacks

reinforce the macroalgal-dominated state and limit the recovery potential of coral populations.

Within coral reef systems, most studies to date have only considered biological agents (i.e., herbivores) for the control and removal of macroalgal biomass (Bellwood et al. 2006a, Ceccarelli 2007, Rasher et al. 2013). However, physical agents such as storms may disrupt the regime of macroalgal-dominated communities by removing large swathes of tall, canopy-forming macroalgae in a single event (Glynn et al. 1964, De Ruyter van Steveninck and Breeman 1987, Rogers 1997, Lapointe et al. 2006). For example, strong storms have been reported to initiate both forward and backward shifts between kelp- and urchin-dominated regimes on temperate Californian reefs (Ebeling et al. 1985). While the reduction in biomass may be immediate and near complete, storms generally break the macroalgae off at the stipe, leaving the holdfast ('root-system') intact on the benthos (Dayton et al. 1984, De Ruyter van Steveninck and Breeman 1987, Underwood 1998). Many macroalgae can regrow from their holdfast (Vuki and Price 1994, Westermeier et al. 2013), potentially allowing the macroalgal biomass to quickly recover to its pre-disturbance abundance. Therefore, in the context of disrupting a degraded, macroalgal-dominated regime, we must consider not only the initial removal of macroalgal biomass, but also the removal of the remaining holdfasts.

On many degraded Indo-Pacific coral reefs, the dominant canopy-forming macroalgae is *Sargassum* spp., a leathery, brown macroalga that can form dense beds and reach heights of 3 m (Hughes et al. 2007, Rasher et al. 2013). The objective of this study was to investigate the resilience of *Sargassum* beds to physical disturbance. Specifically, I quantified (a) how the physical removal of *Sargassum* biomass influences its subsequent density, canopy height, and biomass over 11 months, (b) the relative contribution of newly recruited *Sargassum* and regrowth from holdfasts to

Sargassum biomass, and (c) the capacity of herbivores to damage and/or remove *Sargassum* holdfasts from the benthos.

3.2 Materials and methods

3.2.1 Study site and species

This study was conducted on Orpheus Island (18°35'S, 146°20'E), a continental island situated approximately 15 km from the Queensland coast in the central Great Barrier Reef (GBR), Australia (Appendix B). Orpheus Island has well-developed fringing reefs along its leeward margin and, like many inshore reefs on the GBR, extensive beds of *Sargassum* spp. (up to 2 m in height) on the mid- and outer-reef flats (Fox and Bellwood 2007, Wismer et al. 2009). *Sargassum* spp. (predominantly *Sargassum polycystum, S. fissifolium,* and *S. oligocystum*) is the dominant canopy-forming macroalga on the reef flat at Orpheus Island (e.g., Hughes et al. 2007; Lefevre and Bellwood 2011), with large areas or entire bays often dominated by a single species. Several other canopy-forming phaeophytes, including *Cystoseira trinodis, Hormophysa cuneiformis, Sargassopsis decurrens* and *Turbinaria ornata* are present, but not common, on Orpheus Island.

Sargassum is a highly seasonal macroalga, with patterns of growth, reproduction and senescence linked to changes in water temperature (Lefèvre and Bellwood 2010, Fulton et al. 2014). At Orpheus Island, *Sargassum* grows rapidly from October to February, reaching peak biomass in April, after which it senesces and sheds most of its fronds (late May/June). The lowest biomass occurs in August, when individual *Sargassum* consist of a holdfast and one or two short primary axes <5 cm long (Lefèvre and Bellwood 2010). *Sargassum* has an extended reproductive period that generally coincides with the period of high biomass. While no data is available for

the timing of *Sargassum* reproduction at Orpheus Island, the highest densities of reproductive *Sargassum* thalli at Magnetic Island (an inshore island 60 km south of Orpheus Island) occur between January-April (Martin-Smith 1993).

3.2.2 Resilience of Sargassum to physical removal

To simulate the effect of a storm removing *Sargassum* biomass from the reef, a macroalgal removal experiment was conducted. *Sargassum* assemblages, predominantly *S. polycystum,* were manipulated on the mid-reef flat in two bays: Pioneer Bay and Hazard Bay (Appendix B). Eight sites or 'blocks' were haphazardly selected across the two bays (four blocks per bay), with adjacent blocks separated by a minimum of 40 m. Within each block three 1.5 x 1.5 m plots were haphazardly selected, with at least 2 m between adjacent plots. The corners of each plot were marked with a small metal bar hammered into the substratum and labelled with a small, numbered plastic tag. Each plot within a block was then randomly allocated one of three treatments: (a) 'trimmed': *Sargassum* biomass was removed by cutting the primary axes 1-2 cm above the holdfast to simulate the effect of a storm on *Sargassum* beds, (b) 'removed': each *Sargassum* thallus (i.e., whole plant) within the plot was completely removed using a paint scraper to remove the holdfast from the substratum at the point of attachment, and (c) control: patches in which no macroalgal material was removed. Only *Sargassum* was manipulated within each plot, all other benthic organisms were left intact. No other canopy-forming algae were present in the plots.

The *Sargassum* clearances were initiated in late April and completed in the first week of May, with the timing selected to coincide with recent cyclone activity on the GBR. Specifically, the majority (eight out of ten) of severe tropical cyclones (categories 4 and 5) that have crossed the GBR in the last 12 years have occurred

during March and April (Australian Bureau of Meteorology 2017). This period of high cyclone activity is toward the end of the extended reproductive period of *Sargassum* (Martin-Smith 1993) and coincides with the period of highest *Sargassum* biomass on the GBR (Martin-Smith 1993, Lefèvre and Bellwood 2010).

The height and density of *Sargassum* within each plot was quantified immediately prior to and immediately after the manipulations, and subsequently at 2-monthly intervals from October 2015 to April 2016 (i.e., 5, 7, 9 and 11 months after the initial clearance). These survey intervals were selected to coincide with the period of highest growth for *Sargassum*. To quantify *Sargassum* density, each 1.5 x 1.5 m plot was divided into nine equal 0.5 x 0.5 m quadrats, and each quadrat thoroughly and systematically searched. Within each quadrat, the number of holdfasts (density) and the height of four haphazardly selected *Sargassum* thalli (to the nearest cm) was recorded. If there were four or fewer *Sargassum* thalli within a quadrat, the height of each thallus was recorded. The biomass of *Sargassum* within each plot was estimated using a length-weight relationship for *Sargassum polycystum* based on existing data from Orpheus Island (wet weight (g) = 0.5637 x height (cm), $R^2 = 0.77$; Hoey 2010).

3.2.3 Herbivore-mediated holdfast removal

To assess the potential for herbivores to remove *Sargassum* holdfasts and hence limit their regrowth, I manipulated herbivore access to *Sargassum* holdfasts using exclusion cages. 81 pieces of dead coral or reef pavement (approx. 20 cm in diameter; hereafter referred to as ‘rocks’) with *Sargassum* attached were collected from the mid-reef flat in Pioneer Bay, Orpheus Island in October 2015. Each rock was examined macroscopically and the number and diameter of *Sargassum* holdfasts (measured with callipers to the nearest mm) on each rock was recorded.

Rocks were labelled with a uniquely numbered small plastic tag and 27 rocks were randomly allocated to each of three bays on the leeward side of the island (Hazard Bay, Little Pioneer Bay or Pioneer Bay; Appendix B). Within each bay, rocks were attached to the reef crest using a marine epoxy and randomly allocated to one of three treatments (n = 9 rocks per treatment per bay): (a) caged (44 x 29 x 55 cm, 2 cm square mesh) to prevent access by herbivores, (b) exposed to local herbivorous fish assemblages, or (c) initially exposed to herbivores for six weeks, then caged for the remaining 10 weeks to determine whether fishes could inflict substantial damage over a shorter timeframe.

Experimental rocks were deployed onto the reef crest, as opposed to returning to the reef flat, to avoid any potential interference of dense macroalgae on the feeding behaviour of herbivorous fishes. The reef crest sites were positioned approximately 30 m seaward from the clearance plots on the reef flat in each bay, and the benthic communities resembled what may be expected following a large storm; dominated by reef pavement covered with short filamentous algae, a low cover of live corals, and no canopy-forming macroalgae. Importantly, inshore reef crest and reef flat habitats on the GBR, including those on Orpheus Island, have similar herbivorous fish species composition (dominated by the parrotfish *Scarus rivulatus* and the rabbitfish *Siganus doliatus*), but the reef crest generally supports three to six times greater biomass of herbivorous fishes than the reef flat (Fox and Bellwood 2007, Hoey and Bellwood 2008, Wismer et al. 2009, Hoey et al. 2013). Further, Hughes et al. (2007) demonstrated that the exclusion of herbivorous fishes from large (25 m^2) areas of the reef crest on Orpheus Island led to a proliferation of *Sargassum*, suggesting that environmental conditions are similar between the reef flat and crest. Redeploying the rocks on the reef flat, where canopy-forming macroalgae are abundant, would likely

confound the results as herbivorous fishes have been shown to avoid feeding in dense beds of *Sargassum* (McClanahan et al. 2002, Hoey and Bellwood 2011). All rocks were retrieved after 16 weeks and the number and diameter of holdfasts was recorded as previously described. The presence, form and number of any feeding scars on the rocks were also noted. Twelve of the initial 81 rocks could not be relocated after the 16-week experimental period and were removed from the analysis (see Appendix B).

3.2.4 Statistical analyses

To compare the height and density of *Sargassum* between treatments, blocks and time, linear mixed-effects models allowing for nested random effects were fitted to the data using the package nlme (Pinheiro et al. 2016) in R (R Development Core Team 2016). 'Treatment' and 'Time' were included as fixed effects and ‘Block’ was included as a random effect to account for spatial variance in the density and height of *Sargassum*. The best-fit model was determined using Akaike’s information criterion corrected for small sample sizes (AICc) (Akaike 1973, Sugiura 1978). Quadrats in which *Sargassum* was absent were removed prior to height analysis. The holdfast density data was normalised with a square root transformation, while height data was normalised with a log(x) transformation. An autoregressive correlation structure was used in the height model due to the tendency for height to increase through time. Goodness-of-fit for candidate models was determined using Pearson’s chi-squared test, where the sum of the squared residuals is compared to a chi-squared distribution. The degrees of freedom for the chi-squared distribution were determined by the number of estimated parameters subtracted from the total number of measurements in the data. Tukey’s HSD test in the multcomp package (Hothorn et al. 2008) was used post hoc to compare treatments.

Differences in the number of holdfasts between caged, exposed and initially exposed rocks were assessed using a mixed-effects generalised linear model with a Poisson distribution using lattice (Sarkar 2008), lme4 (Bates et al. 2014) and car (Fox and Weisberg 2011) packages in R. 'Treatment' and 'Date' were included as fixed factors and 'Location' was included as a random factor.

3.3 Results

3.3.1 Resilience of Sargassum to physical removal

Prior to the manipulations of *Sargassum* biomass, the height and density of *Sargassum* did not differ among treatments (density: $F_{2,21} = 0.02$, $p = 0.98$; height: $F_{2,21} = 0.19$, $p = 0.83$, Fig. 3.1). The response of *Sargassum* to physical disturbance showed marked differences among treatments, with the density, height and biomass of *Sargassum* within removed plots being lower than those of the trimmed and control plots from 5 to 11 months post-clearance (Fig. 3.1; Appendix B; Tukey's HSD: $p < 0.01$). The best model for height was additive and included an autoregressive correlation structure to account for the tendency for the height of the *Sargassum* to increase through time. The model with the lowest AICc for holdfast density was additive and did not include an autocorrelation structure (Appendix B). The density of holdfasts did not differ between the trimmed and control plots, increasing from 26 to 38 and 27 to 34 holdfasts m^{-2}, respectively, over the 11-month period (Fig. 3.1a). In contrast, the density of holdfasts in the removed plots increased rapidly from 0 to 25 holdfasts m^{-2} at 7 months post-clearance, after which there was little change in density (Fig. 3.1a). At the conclusion of the experiment, the density of holdfasts within the removed plots was 22 and 29 % lower than those in the control and trimmed plots, respectively (Fig. 3.1a; Appendix B), a density only slightly lower than the initial control values.

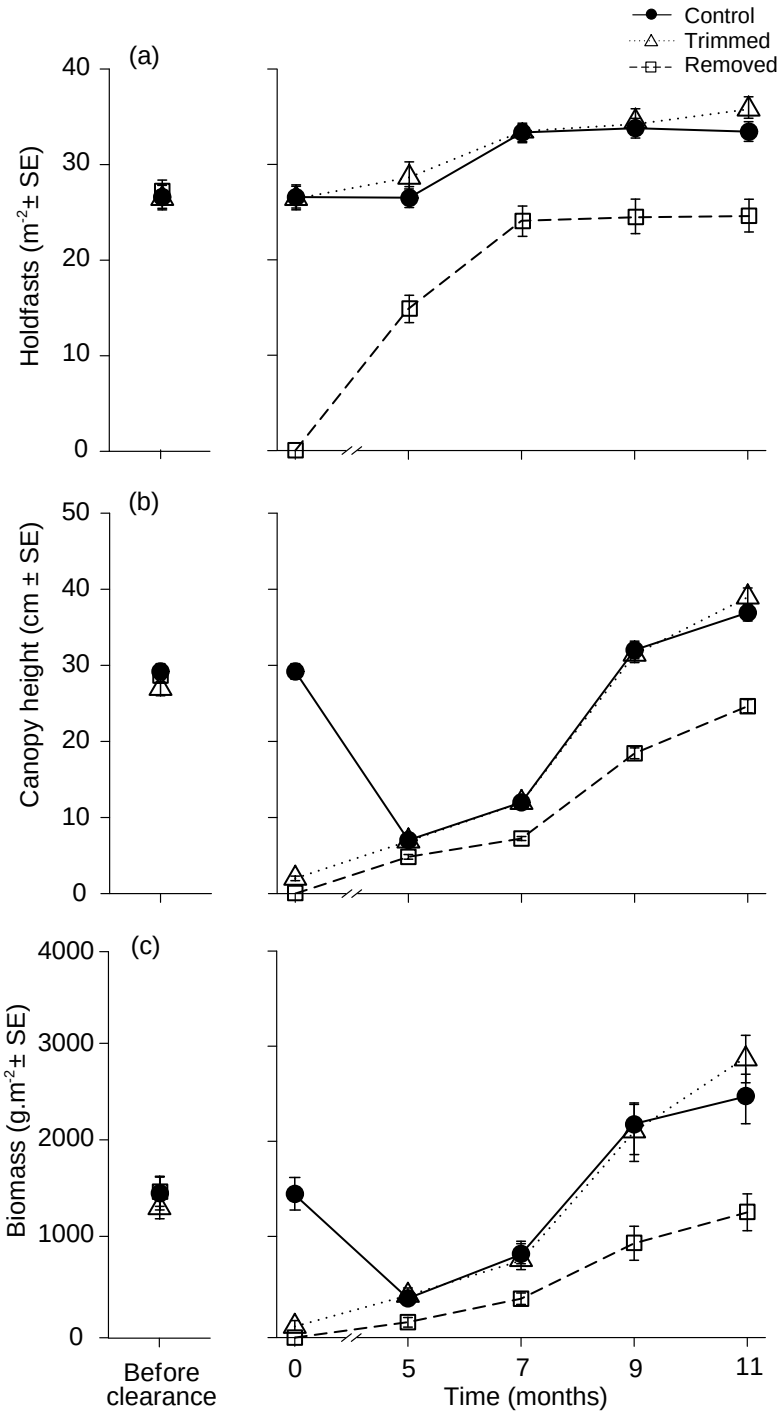

Figure 3.1: Regrowth of *Sargassum* following physical removal of biomass. (a) Number of *Sargassum* holdfasts (m^{-2} ± SE); (b) Average height of *Sargassum* per plot (cm ± SE); (c) Biomass of *Sargassum* ($g.m^{-2}$ ± SE). "Trimmed": *Sargassum* primary axes were cut above the holdfast and holdfasts remained undamaged. "Removed": all *Sargassum* including holdfasts were removed from plots. "Control": no manipulation of the *Sargassum*. Measurements are from immediately pre- and post-clearance (0 months, May 2015) to 11 months post-clearance (April 2016).

The height of the *Sargassum* increased in all treatments over the 11-month period, with the height of *Sargassum* in trimmed and control plots being higher than *Sargassum* in the removed plots (Fig. 3.1b; Appendix B). The mean height of the *Sargassum* canopy in the control and trimmed plots was almost identical throughout the 11-month period, ranging from 7.0 ± 0.4 and 7.0 ± 0.5 cm, respectively, at 5 months post-clearance, to 37 ± 1.1 and 39 ± 1.2 cm at 11 months post-clearance (Fig. 3.1b). The height of the *Sargassum* within the removed plots was 2 cm lower than *Sargassum* in the control or trimmed plots at 5 months post-clearance and increased at a slower rate, resulting in a 13 cm lower mean height of *Sargassum* within the removal plots than the trimmed or control plots at the conclusion of the study.

Combining the density of holdfasts and mean canopy height to estimate *Sargassum* biomass within each plot revealed that 11 months after the clearances, removed plots had an average biomass of 1164 $g.m^{-2}$, approximately half that of the trimmed (2590 $g.m^{-2}$) and control (2311 $g.m^{-2}$) plots (Fig. 3.1c).

3.3.2 Herbivore mediated holdfast-removal

Prior to deployment, the number of holdfasts per rock was similar across all treatments, with an average of 1.9 ± 0.2 holdfasts per rock (Fig. 3.2). Exposing holdfasts to herbivores on the reef crest for 16 weeks led to a significant reduction in the average number of holdfasts (0.55 holdfasts $rock^{-1}$ ± 0.20) compared to those that were protected from herbivores (1.73 holdfasts $rock^{-1}$ ± 0.21) (Fig. 3.2 and Appendix B; χ^2= 6.39, df = 2, $p < 0.05$). The number of holdfasts on 'initially uncaged' rocks (i.e., those only exposed to herbivory for six weeks) was similar to the number on uncaged rocks (i.e., those exposed for the entire 16-week period), averaging 0.63 ± 0.14 holdfasts per rock. Bite scars resembling those of scraping parrotfishes were observed on 8 of the 20

uncaged rocks at the conclusion of the experiment, with the number of scars per rock ranging from 1 to 52. No bite scars were visible on the remaining holdfasts on the herbivore-exposed rocks. All of the holdfasts that remained at the end of the 16-week period had increased in size (Appendix B).

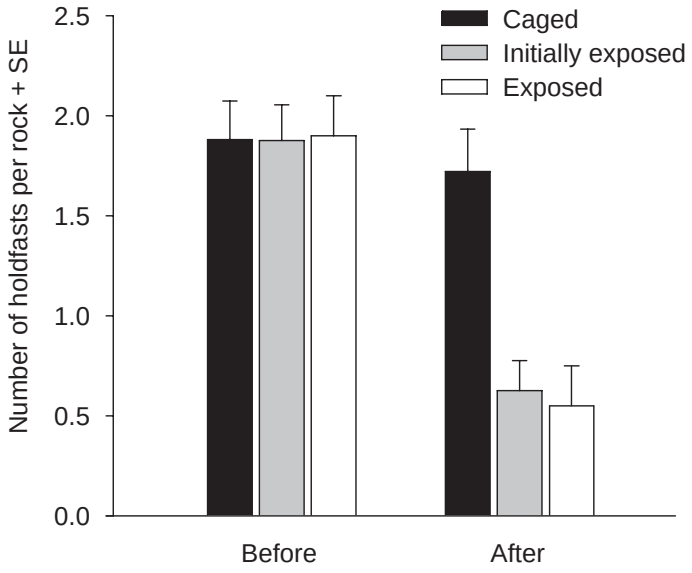

Figure 3.2: Average number of holdfasts per rock before commencing the experiment (October 2015) and 16 weeks later at the conclusion of the study (February 2016). Initially exposed rocks were only subject to herbivory for 6 weeks. All values are mean + SE.

3.4 Discussion

Using an experimental approach to simulate storm-induced mechanical removal of *Sargassum*, I demonstrate that *Sargassum* beds are remarkably resilient to physical disturbance, especially when holdfasts are left intact on the benthos. *Sargassum* biomass recovered rapidly in areas in which biomass was removed but holdfasts remained intact and was indistinguishable from adjacent 'natural' patches of *Sargassum* after five months. Even in areas where the entire alga (including holdfast) was removed, the biomass of *Sargassum* recovered to ~50 % of the biomass of natural patches within 11 months. Importantly, any physical disturbance or biological agent

(i.e., herbivory) that removes *Sargassum* biomass but leaves the holdfast intact is unlikely to initiate a shift away from macroalgal dominance. The removal of macroalgal holdfasts, coupled with the removal of any new macroalgal recruits, will be crucial to long-term reductions in macroalgal biomass on coral reefs.

3.4.1 Recovery from disturbance

Sargassum beds were remarkably resilient to the mechanical removal of biomass when holdfasts were left intact on the benthos (i.e., trimmed plots). This is perhaps not surprising given that *Sargassum* typically exhibit seasonal patterns of growth and senescence (Vuki and Price 1994, Lefèvre and Bellwood 2010, Fulton et al. 2014). Indeed, the reduction in canopy height and biomass within the control plots after five months almost certainly reflects the natural senescence of *Sargassum* at our study sites. Most species of *Sargassum* senesce after reproducing and regrow from the remaining holdfast several months later (e.g., Umar, McCook & Price 1998). This innate ability to regrow from holdfasts affords *Sargassum* the capacity to rapidly recover from disturbances that leave holdfasts intact, as demonstrated by the rapid recovery of *Sargassum* biomass in our trimmed and control plots. Therefore, any disturbance, either biological or physical, that does not remove holdfasts is unlikely to affect the biomass of *Sargassum* over longer temporal scales (i.e., months to years).

The timing of the present study was selected to simulate recent cyclone impacts on the GBR, and as a consequence, did not investigate how the timing of a disturbance may affect the recovery of *Sargassum* biomass. However, clearance studies performed in temperate macroalgal beds report that recovery of the canopy can vary depending on the season in which the macroalgae are removed, predominantly due to the differing growth of juveniles in the understory (Kennelly 1987, Tanner 1995, Toohey and

Kendrick 2007). The seasonality and quantity of propagules, as well as the ability of a species to regrow vegetatively, have been demonstrated to strongly influence the rate at which a community will return to its pre-disturbance composition (Sousa 1980). Recent cyclone activity on the GBR has been concentrated in early autumn (i.e., March and April), after the peak reproduction in *Sargassum* (Martin-Smith 1993). As such, *Sargassum* propagules released during the preceding summer's reproduction are likely to be already present on the benthos, and appeared to have contributed to the recovery of biomass within the removed plots. Recovery may, therefore, be reduced if a disturbance occurred prior to *Sargassum*'s reproductive period (i.e., November/December). However, no severe cyclones have crossed the GBR prior to January in the past 12 years (Australian Bureau of Meteorology 2017).

Comparisons of the accumulation of *Sargassum* biomass between removed and trimmed plots provide an indication of the relative contribution of new recruits versus regrowth from holdfasts to *Sargassum* biomass. The holdfasts of *Sargassum* growing in removed plots were noticeably smaller than those of the *Sargassum* in trimmed or control plots (ZL pers. obs), and are likely due to the growth and survival of propagules released during *Sargassum*'s summer reproduction (Martin-Smith 1993, Kendrick and Walker 1994). The density of *Sargassum* increased by ~25 holdfasts m^{-2} within the removed plots during the study, compared to ~12 holdfasts m^{-2} in the trimmed plots. This suggests that the growth and survival of juvenile *Sargassum* is suppressed under the canopy of adult *Sargassum*. Such suppression of the growth of juvenile plants in the understory is widespread and has been demonstrated in terrestrial forests (Canham 1988, Denslow 1995) and temperate and subtropical macroalgal beds (Kirkman 1981, Kendrick 1994, Kinlan et al. 2003, Toohey and Kendrick 2007). For example, Kendrick and Walker (1994) found that three-times more *Sargassum* recruits survived their first

year in areas cleared of adults, compared to uncleared controls on a subtropical reef, and suggested that *Sargassum* propagules may be able to exist in an extremely slow-growing state in the understory. *Sargassum* propagules present on the benthos appear to act much like many seedlings in terrestrial systems: light limited under thick conspecific canopies but capable of rapid growth when adults are not present (Kendrick 1994, Szwagrzyk et al. 2001). The capacity of recruits for rapid growth was evident in the relatively small (13 cm) height difference between adults in trimmed plots and the juvenile 'new recruits' that would have grown from a microscopic size without the aid of stored resources in their holdfast (Wong 2007). Thus, whilst adult holdfasts are pivotal in the recovery of *Sargassum* beds following disturbance, the potential role of *Sargassum* recruits should also be considered.

The limited impact of our experimental clearances on *Sargassum* biomass indicates that physical disturbances, such as storms that leave holdfasts intact on the substratum (Dayton et al. 1984, De Ruyter van Steveninck and Breeman 1987, Underwood 1998), are unlikely to provide an opportunity for the establishment and growth of corals. The peak reproduction for scleractinian (hard) corals on the GBR typically coincides with moderate to high cover of *Sargassum.* For example, most corals on inshore reefs on the Great Barrier Reef spawn in November (Babcock et al. 1986) and settle within 2-3 weeks, coinciding with an estimated *Sargassum* biomass of 700 $g.m^{-2}$ (7-months post-clearance in the present study). Any corals that did settle would be unlikely to reach a size within the next 6-12 months at which they could outcompete the regenerating macroalgae (Box and Mumby 2007, Birrell et al. 2008a). Furthermore, if a significant storm occurred prior to this coral spawning event and opened up space on the benthos for the settlement of coral, it would also likely damage corals and hence reduce the potential spawning stock (Madin and Connolly 2006).

3.4.2 Herbivore mediated holdfast-removal

The rapid regrowth of *Sargassum* in trimmed plots highlights the importance of the holdfast to the resilience of *Sargassum* to disturbance. While physical disturbances are unlikely to dislodge holdfasts from the substratum (Dayton et al. 1984, De Ruyter van Steveninck and Breeman 1987), they may be damaged or removed by organisms that scrape the substratum when feeding. Indeed, there was a marked reduction in the number of holdfasts on rocks exposed to herbivores on the reef crest compared to caged controls. This result provides evidence that herbivores are capable of removing *Sargassum* holdfasts from the benthos and, in areas where herbivores are abundant, potentially reducing the dominance of *Sargassum* on degraded reefs.

The reduction in the number of holdfasts exposed to local herbivore assemblages appears likely due to the action of parrotfishes. Although feeding on the holdfasts was not directly quantified in the current study, both parrotfishes and sea urchins scrape and/or excavate the reef substratum when feeding (Bonaldo et al. 2014), and thereby likely have the ability to damage and/or completely remove *Sargassum* holdfasts from the benthos. Parrotfishes are abundant on the reef crest and reef flat at the study site where they comprise upwards of 80 % of the herbivorous fish biomass (Bellwood et al. 2006a, Fox and Bellwood 2007). The scarcity of sea urchins on the GBR (Done et al. 1991) and at our study sites in particular (<3 urchins 100 m^{-2}, Hughes et al. 2007), coupled with numerous distinctive parrotfish bite scars on several of our experimental rocks exposed to herbivores, indicates that parrotfishes were likely responsible for the removal of holdfasts. Although parrotfishes have the physical capacity to remove holdfasts, I cannot be certain if the observed removal was due to targeted or incidental feeding (Clements et al. 2016).

It should be noted that the experimental approaches used in this study, and other studies, do not replicate all likely impacts of severe storms on biological communities. The impacts of a storm on benthic communities will vary depending on the strength and direction of the storm and the composition of the substratum (Woodley et al. 1981, Harmelin-Vivien 1994, Fabricius et al. 2008, Beeden et al. 2015). While the present study simulated the likely effect of a storm on a *Sargassum* community on consolidated substratum, the impact may be different for communities on unconsolidated substratum (i.e., rubble). Storms are likely to overturn and redistribute unconsolidated substrata, reducing the growth and survival of any attached algal propagules and coral recruits (Rogers 1990, Harmelin-Vivien 1994, Umar et al. 1998, Fabricius et al. 2003). Together with potential differences in the characteristics of the underlying substratum, a storm will impact an area considerably larger than the size of our experimental plots (i.e., 2.25 m^2). It could be argued that shading and/or changed hydrodynamics due to the surrounding *Sargassum* canopy, or the subsequent release of propagules from intact *Sargassum* adjacent to the plots, could have influenced the recovery of *Sargassum* biomass with our plots. While I cannot rule out these potential effects, they seem unlikely. The vast majority (up to 96 %) of *Sargassum* propagules settle within 0.25 m of the parent plant (Kendrick and Walker 1991, Stiger and Payri 1999) and effects of shading are likely to be greatest immediately adjacent to the intact *Sargassum*. As such, any potential effects of plot size may manifest as a lower density of holdfasts in the centre of the experimental plots compared to the edges, and/or changes in *Sargassum* biomass between the centre and edges of the plots. Comparisons of the size and density of *Sargassum* within each plot revealed there were no differences between the centre and edge of each plot.

At a time when many coral reefs around the world are under significant stress (Hughes et al. 2017b), identifying ways to reduce the feedbacks reinforcing the dominance of macroalgae on degraded reefs is becoming increasingly important. Worryingly, *Sargassum,* the dominant macroalga on many degraded Indo-Pacific reefs, appears to be exceedingly resilient to disturbance. The physical removal of *Sargassum* biomass alone, whether by storms or biological agents, will have a limited impact on the composition of the benthic community because of *Sargassum*'s ability to rapidly regrow from holdfasts. Even when the entire thallus including holdfast was experimentally removed, *Sargassum* returned to dominate the benthic community within a year. The resilience of *Sargassum,* coupled with the positive feedbacks that limit the recovery of coral populations (Mumby and Steneck 2008, van de Leemput et al. 2016) highlight the difficulties in initiating a shift back toward coral dominance on degraded reefs. Critically, there must be a corresponding change to an underlying parameter, such as herbivory, if a disturbance is to shift the system away from a macroalgal-dominated state. While the ability to regrow from holdfasts and rapid growth rates may make canopy-forming macroalgae particularly resilient to acute disturbances, shifts away from degraded regimes in other ecosystems have generally occurred when reductions in one or more chronic stressors are coupled with an acute disturbance that impacts the dominant habitat-forming organism, essentially resetting the system (Holmgren and Scheffer 2001, Anderies et al. 2002). Efforts to return ecosystems from degraded regimes to more desirable regimes will require a coordinated approach that breaks the reinforcing feedbacks and reduces or removes stressors that contributed to the initial decline.

Chapter 4: Holdfasts of *Sargassum swartzii* are resistant to herbivory and resilient to damage[3]

4.1 Introduction

Coral cover is declining in all major reef regions, largely due to the combined effects of global climate change and local anthropogenic stressors (De'ath et al. 2012, Heron et al. 2016, Hughes et al. 2017b). This reduction in coral cover often leads to an expansion of the cover of algae and other organisms (Norstrom et al. 2009) that rapidly colonise the dead coral skeletons (Diaz-Pulido and McCook 2002). Reefs with relatively intact herbivore assemblages appear to be able to compensate for this increased algal production, maintaining algal communities in a cropped state and facilitating the recovery of coral assemblages (e.g., Adam et al. 2011; Gilmour et al. 2013). However, on reefs where herbivore assemblages have been reduced, the capacity to absorb the increased algal production is compromised, releasing algal communities from top-down control that may ultimately lead to a new regime dominated by fleshy brown macroalgae, such as *Sargassum* (Bellwood et al. 2004, Mumby and Steneck 2008). Such regime shifts represent a fundamental change in habitat structure and functioning, and once established can be difficult to reverse (Scheffer et al. 2001, van de Leemput et al. 2016, Harborne et al. 2017).

The apparent stability of macroalgal-dominated regimes has been attributed to a range of positive feedbacks that enhance macroalgal growth and/or limit the

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replenishment and recovery of scleractinian corals (Hughes et al. 2007, Mumby and Steneck 2008, Hoey and Bellwood 2011, Dell et al. 2016, van de Leemput et al. 2016). For example, herbivorous fishes have been shown to avoid dense stands of macroalgae, which in turn, may lead to further expansion of the macroalgae (Hoey and Bellwood 2011). The settlement of coral larvae, and the growth and survival of corals, are inhibited by the presence of macroalgae (Venera-Ponton et al. 2011, Webster et al. 2015) and can potentially lead to further declines in coral cover and expansion of macroalgae (Hughes and Tanner 2000). The presence of these feedbacks suggests that removal of established macroalgae in reef habitats will require greater levels of herbivory than those initially required to prevent macroalgae from becoming established (Mumby et al. 2007, van de Leemput et al. 2016). However, the capacity of herbivores to initiate a change from a macroalgal-dominated regime toward a coral-dominated regime is likely to depend not only on the overall rate of herbivory, but also the specific nature of herbivory. Notably, the species of herbivores (and their specific functions) that are necessary to reverse regime shifts are different to those that prevent the initial proliferation of macroalgae (Bellwood et al. 2004).

Herbivorous reef fishes may be broadly classified into two groups, macroalgal browsers and grazers. Macroalgal browsing fishes typically consume large, fleshy macroalgae, such as *Sargassum*, and have been suggested to be important in potentially reversing macroalgal-dominated regime shifts (Bellwood et al. 2006). In contrast, grazing fishes typically feed on the Epilithic Algal Matrix (EAM) and are thought to play an important role in the prevention of shifts to macroalgal dominance by consuming small macroalgal propagules growing within the EAM (Bellwood et al. 2004, Mumby 2006). Previous research has shown that while the removal of macroalgal biomass by browsers can be rapid, it is dependent upon the actions of a

limited number of species; grazing fishes appear to be largely incapable of removing large fleshy macroalgae from the reef (Hoey and Bellwood 2009). Although this distinction is important, these studies have not considered the capacity of herbivores to remove different components of the macroalgae (but see Streit et al. (2015)) and rarely consider the ecology of the macroalga itself. Importantly, the capacity of herbivores to remove the macroalgal holdfast has never been considered, despite the ability of some macroalgae such as *Sargassum* to regrow from holdfasts when the stipes and blades are removed (Ang Jr 1985, Vuki and Price 1994, Loffler and Hoey 2018). Investigating the capacity of herbivores to damage and/or remove macroalgal holdfasts, and the effect of holdfast damage on the subsequent growth and survival of the macroalgae is critical to further understanding the feedbacks maintaining and expanding macroalgal communities.

The purpose of this study was to investigate rates of herbivory on different components of *Sargassum swartzii* thalli, specifically comparing the rate and extent of removal of blades, stipes and holdfasts for thalli translocated into areas with high levels of herbivory. I also investigated the resilience of *S. swartzii* to physical damage of holdfasts, testing whether increasing levels of experimental damage (up to 75 % removal of the area of holdfasts) impacted the survival and size of individuals during the next growing season.

4.2 Materials and methods

4.2.1 Study sites

This study was conducted over one year (November 2016 to November 2017) at both the mid-shelf reef of Lizard Island (14°40′S, 145°28′E) and the inner-shelf reefs of the Turtle Group (14°43′S, 145°12′E) in the northern Great Barrier Reef (GBR), Australia

(Appendix C). Lizard Island is a granitic island in the northern GBR. The Turtle Group Islands are approximately 28 km west of Lizard Island and 11 km from the mainland coast. The fringing reefs surrounding the islands in the Turtle Group are characterised by low coral cover on the south-east and north-east aspects with large beds of *Sargassum* (up to 1.5 m tall) at depths less than 3 m (Hoey and Bellwood 2010a). *Sargassum* spp. is rare at Lizard Island, but does occur in areas of low herbivory, such as in damselfish territories (Hoey and Bellwood 2010b) and on the reef flat (A.S. Hoey pers. obs.).

4.2.2 Herbivory of S. swartzii

To compare rates of herbivory between the major components of *Sargassum* (blade, stipe, and holdfast) and to identify the species responsible, I exposed assays of whole *Sargassum swartzii* thalli to local herbivore assemblages on Lizard Island and recorded any feeding using stationary underwater video cameras. Twenty-four pieces of reef substrate with attached *S. swartzii* thalli were collected from the Turtle Group reefs using a hammer and chisel (carbonate pavement; 15-20 cm diameter) to ensure holdfasts were collected in their entirety. Each piece of reef substrate had between 1 and 4 individual *S. swartzii* thalli attached. The combination of *S. swartzii* thalli attached to a piece of reef pavement is hereafter referred to as an ‘assay’. These assays were transported back to Lizard Island Research Station within 3 h of collection and placed in a 1000 L aquarium (2 × 1 × 0.5 m) with flow-through seawater and supplemental aeration. The number of *Sargassum* thalli, the height of each thallus and the diameter of its corresponding holdfast were recorded, and each assay labelled with a small numbered plastic tag. For each holdfast, I recorded the maximum diameter and

perpendicular diameter to the nearest 0.1 mm using callipers. Assays were deployed within 48 h of collection.

To quantify the rate and extent of herbivory, assays were deployed at two reef crest sites (2-3 m depth) exposed to the prevailing south-easterly winds (Appendix C). Twelve randomly selected assays were placed at each site, with eight exposed to local herbivore assemblages and four placed inside herbivore exclusion cages to control for the effects of handling, translocation and survival of the *S. swartzii* over the 24-day experimental period. Each assay was secured to a 20 × 20 × 4 cm paving tile using a cable tie, placed on an area of bare substratum (i.e., covered by turf algae yet free of live coral and other macroinvertebrates) and secured to the reef with thin galvanised wire (0.5 mm) threaded through natural holes in the reef (Appendix C). This method was used because pilot experiments demonstrated that cable ties were too wide to thread through natural holes in the reef, and assays attached directly to the reef using wire were less tightly secured than assays attached to paving tiles with cable ties. Exclusion cages (40 × 30 × 30 cm with 1 cm^2 mesh) were secured over control thalli and held in place with lead weights that were cable tied to the bottom corners of each cage. All assays were positioned at a similar depth (2-3 m) with a minimum of 2 m between adjacent assays.

To estimate the reduction in *S. swartzii* biomass during the experimental period, each assay exposed to herbivores was photographed every 1-4 days (weather dependent) for the first 19 days and again after 24 days. A 30 cm ruler was held adjacent to each assay to provide a scale for quantifying blade area. Photographs of caged assays (i.e., controls) were taken at the beginning and end of the experimental period. The total surface area of the *S. swartzii* was estimated by tracing around it in the photographs using the program ImageJ, and for each replicate, the components

remaining (i.e., blades, stipes, and holdfast) were recorded. By quantifying changes using photographs, I minimised handling and disturbance during the experimental period.

To identify the fishes responsible for removal of *S. swartzii* blades and stipes, and any fishes grazing on the experimental rocks, a small remote underwater video camera (GoPro) attached to a dive weight was placed ~1 m from each uncaged rock. The video cameras were deployed once per day (between 08:00 and 09:00, for 3.5 h) on the first 3 days and every 2-4 days thereafter (weather dependent), until day 19 (9 days of video per rock). No video was taken between day 20 and the conclusion of the experiment (day 24). After 24 days, the rocks were collected and the diameter of remaining holdfasts and the height of any remaining *S. swartzii* thalli were re-measured as previously described.

The entire video footage (~ 450 h) was analysed and each fish larger than 10 cm that took bites on the *S. swartzii* thallus and/or experimental 'rock' was recorded. Fishes smaller than 10 cm were not included due to difficulties in accurately quantifying individual bites and/or identifying individuals to species. Due to difficulties in determining whether fishes observed taking bites from the surface of the rock were biting the *S. swartzii* holdfast or adjacent to the holdfast, all bites on the rocks were recorded.

4.2.3 Carbon and nitrogen content of S. swartzii components

To determine whether any differences in feeding could be related to the elemental composition of the *S. swartzii* components, the carbon and nitrogen content of the *S. swartzii* tissues were analysed. Samples of holdfasts, stipes and blades were taken from five distinct *S. swartzii* thalli collected from the Turtle Group and freeze-dried for 48 h.

Samples (min. 0.2 g dry weight) were then sent to OEA Laboratories LTD, UK to quantify carbon and nitrogen content using an elemental analyser, giving the percentage of carbon and nitrogen as grams per 100 g dry weight (% dw).

4.2.4 Survival and regrowth of damaged S. swartzii holdfasts

To determine if damage to a holdfast affects the subsequent survival and regrowth of the thallus, four levels of damage were inflicted on holdfasts of *S. swartzii* in November 2016 and their condition monitored after 12 months. Two sites on the leeward aspect of reefs in the Turtle Group were selected. These two sites were characterised by numerous shallow bommies densely covered with *S. swartzii* and interspersed with areas of sand and coral rubble. At each site, three 4 m^2 patches of *S. swartzii* of similar height were haphazardly selected, with at least 4 m between adjacent patches. Within each patch, all *Sargassum* were cut with scissors just above the holdfast. A small numbered tag was attached to the substratum with a galvanised nail next to each holdfast to allow individual holdfasts to be identified. Any other holdfasts within a 10 cm radius of the tag and experimental holdfast were removed using a hammer and chisel. The diameter of the tagged holdfasts was measured (using the same method previously described), photographed and haphazardly allocated to one of four treatments: (a) control (not manipulated/damaged), (b) 25 % of holdfast removed, (c) 50 % of holdfast removed and (d) 75 % of holdfast removed. As a result of removing 75 % of the holdfast, the original point of stipe growth was removed in this treatment but was not entirely removed in any of the other treatments. A Stanley knife was used to make a vertical cut through the holdfast, and the ‘offcut’ (either 25, 50 or 75 %) was then scraped off the substratum, being careful not to disturb the remaining portion of

the holdfast. A photograph of the holdfast was also taken after the damage was inflicted, to facilitate re-identification.

After 12 months (i.e., November 2017) each experimental patch was systematically searched and the remaining tags and holdfasts identified. If there was no holdfast within 10 cm of a tag, the individual was recorded as dead. For each surviving holdfast, the height of its thallus was measured to the nearest centimetre using a tape measure and the diameter of the holdfast was measured as described above. A photograph was taken of the holdfast and its corresponding tag. All before and after photographs were examined to ensure that the correct holdfast had been identified and measured. The loss of some tags led to an unbalanced design, with the tags corresponding to 14 control, 16 25%-removed, 22 50%-removed and 27 75%-removed treatments remaining.

4.2.5 Statistical analyses

All statistical analyses were conducted using R version 3.4.1. R packages rstan and rstanarm were used to run Bayesian analyses. All models used Gaussian distributions. Weakly informative priors were used, with 5000 iterations, a warmup of 2500, three chains and a thinning factor of five. Diagnostic plots were analysed to ensure there was convergence of chains, no autocorrelation and that priors were sufficiently wider than the posterior values. All Rhat values were < 1.05 and ESS values were > 0.6.

To compare the size of holdfasts before and after deployment between caged and exposed thalli, a Bayesian generalised linear model was used, with date and treatment included as fixed factors. Differences in elemental composition (i.e., carbon and nitrogen content) among components of the *S. swartzii* were analysed with Bayesian generalised linear mixed effects models. Component (holdfast, stipe or blade)

was included as a fixed factor with each *S. swartzii* used as a random factor to account for any differences among *S. swartzii* individuals. Any differences in the survival, holdfast diameter or thallus height of damaged holdfasts among treatments 1 year after damage was inflicted was analysed using Bayesian generalised linear mixed effects models. Damage inflicted was included as a fixed factor and patch was included as a random factor.

4.3 Results

4.3.1 Herbivory of S. swartzii

Within 2 days of deployment, all blades had been removed from all thalli exposed to herbivores, corresponding to an 88 % decrease in surface area, from 320 ± 31 cm^2 on day one to 40 ± 7 cm^2 on day two (Fig. 4.1a). Thereafter, the surface area of the thalli decreased slowly, from 22 ± 4 cm^2 on day three to 7 ± 2 cm^2 on day 19. After 24 days the majority of assays (72 %) still had partial stipes present and only 28 % of assays had stipes completely removed (Fig. 4.1c). Only one holdfast (out of 53) was removed after 24 days of exposure to local herbivore assemblages. For caged controls, surface area and height of assays decreased by 27.5 % and 28.9 %, respectively, over the course of the experiment. All control thalli had holdfasts, stipes and blades remaining at the conclusion of the experiment.

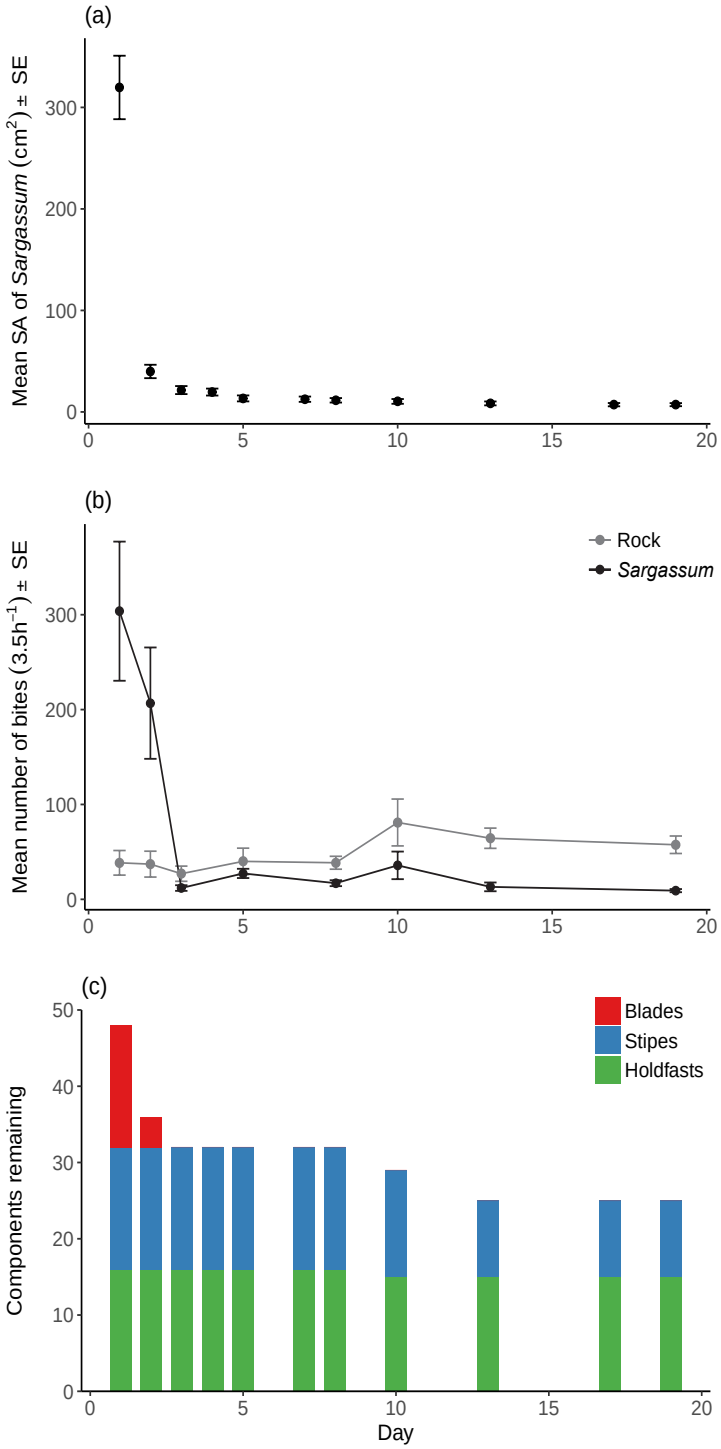

Figure 4.1: (a) Mean surface area (SA) of *Sargassum swartzii* thalli throughout experiment ± SE; (b) Mean number of bites in 3.5 h on deployed rocks and their attached *S. swartzii* thalli, ± SE; (c) Components of exposed *S. swartzii* thalli remaining throughout the study: there were 16 assays exposed to herbivores (i.e., for day one, 16 assays × 3 components = 48). Experiment was concluded after 24 d, however, feeding observations (i.e., video footage) were only taken to day 19. No further removal of components occurred between day 19 and day 24.

Video analysis revealed that the rapid consumption of the blades of the *Sargassum* in the first 2 days of deployment was primarily due to the feeding by two fish species: *Naso unicornis* and *Siganus doliatus* (Figs. 4.1b, 4.2). These fishes took 66 and 17 % of total bites on the *S. swartzii*, respectively, on the first 2 days of deployment. Bite rates on the *S. swartzii* decreased markedly once the blades had been removed. For example, *Naso unicornis* took 98 % of its bites in the first 2 days, when the *S. swartzii* thalli had blades remaining.

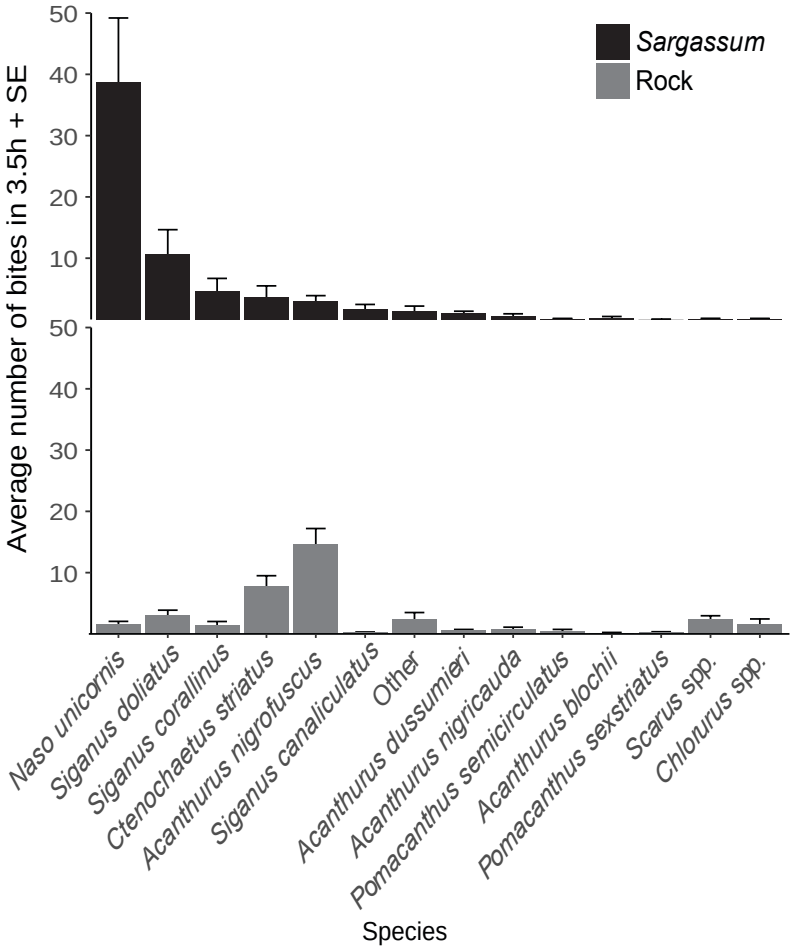

Figure 4.2: Average number of bites taken on assays in 3.5 h of video over the course of the experiment. Fish species are ordered by the number of bites on *Sargassum swartzii*. For full list of species and their corresponding bite count, see Appendix C.

The number of bites taken on the surface of the experimental rocks increased from an average of 39 ± 13 bites 3.5 h^{-1} on day one, to 81 ± 25 bites 3.5 h^{-1} on day ten before

dropping to 58 ± 9 bites 3.5 h^{-1} on the last day of video (day 19; Fig. 4.1b). The majority of bites were taken by two surgeonfishes, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* (taking 40 and 21 % of total bites on the rocks, respectively; Fig. 4.2). Bites by parrotfishes accounted for 11 % of total bites, with *Scarus niger* and *Chlorurus spilurus* being the predominant parrotfish species (4 and 3 % of total bites, respectively; Appendix C). Evidence of feeding (i.e., parrotfish feeding scars) on the rocks was variable; some rocks were highly grazed (Fig. 4.3), yet others had few grazing scars. Interestingly, feeding marks were concentrated on the rocks, with little evidence of grazing scars on holdfasts, suggesting that fishes may have avoided feeding on the holdfasts (Fig. 4.3). Indeed, none of the exposed holdfasts remaining at the end of the experiment decreased in diameter compared to controls (Appendix C).

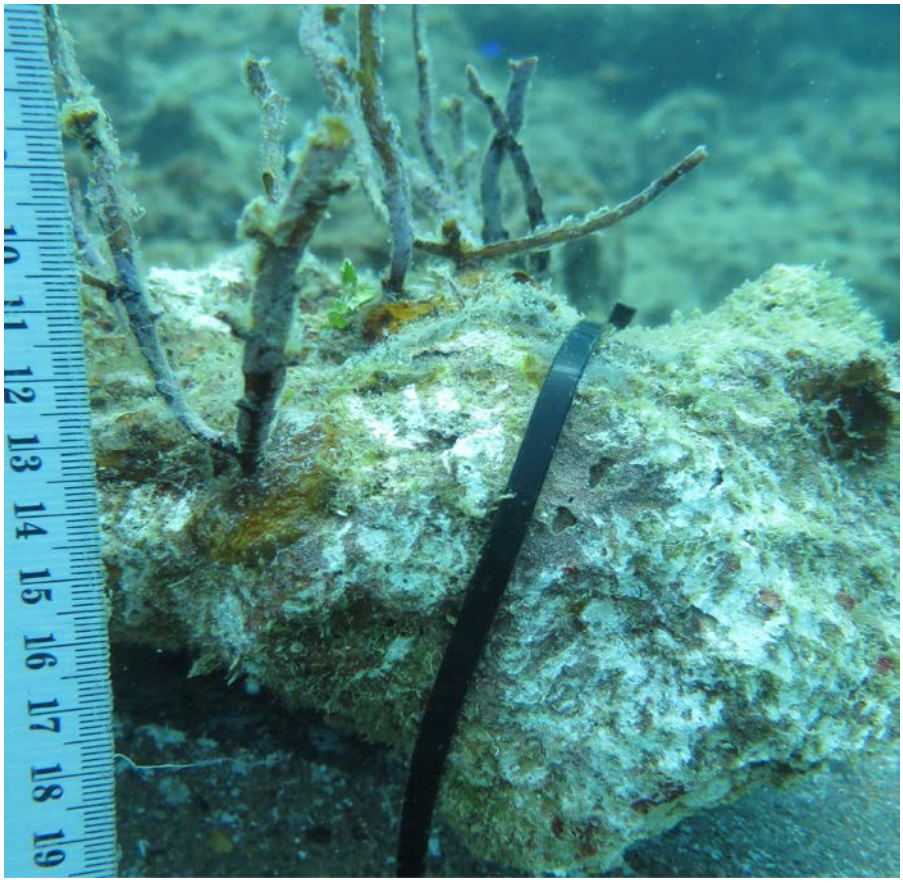

Figure 4.3: Example of grazing scars surrounding the holdfast on rocks exposed to herbivory. This photograph was taken 4 d after deployment. At the conclusion of the experiment, stipes had been

removed from this rock, however, the holdfasts remained intact and had not decreased in size, despite the high grazing impact on the rock.

4.3.2 Carbon and nitrogen content of S. swartzii components

The nitrogen content of *S. swartzii* differed among components, with the holdfasts (0.81 [0.72, 0.92] % dw, mean and 95 % credible intervals), and blades (0.81 [0.74, 0.87] % dw) having greater nitrogen content than the stipes (0.48 [0.38, 0.59] % dw; Fig. 4.4, Appendix C). The carbon content of holdfasts was highest at 33.4 [32.2, 34.4] % dw, with stipes and blades lower at 30.4 [29.3, 31.4] and 28.6 [27.7, 29.4] % dw, respectively (Appendix C). This meant that the holdfasts and blades had similar C:N ratios of 42 [35, 49] and 36 [31, 41], respectively, while the stipes had a ratio of 64 [57, 71] (Appendix C).

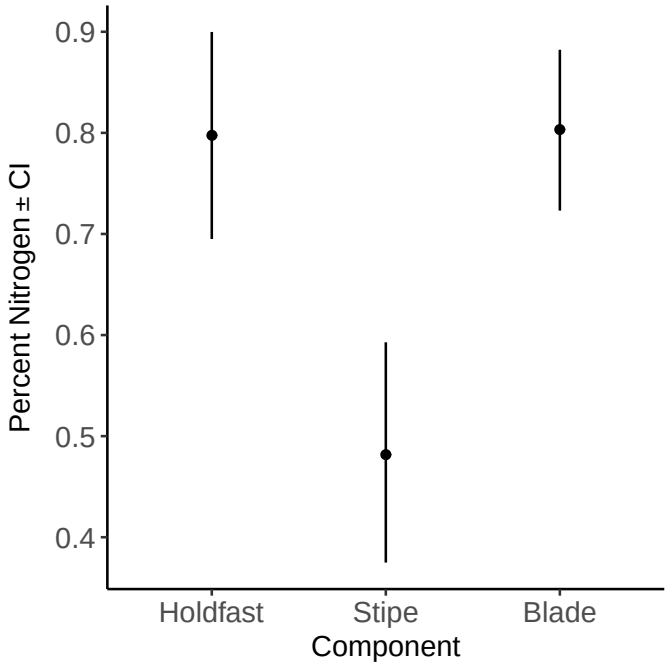

Figure 4.4: Percent nitrogen in *Sargassum swartzii* components, presented as mean ± 95 % credible intervals. The stipe component had a significantly lower nitrogen content than the holdfast and blade components.

4.3.3 Survival and regrowth of damaged S. swartzii holdfasts

Experimentally imposed damage to holdfasts of *S. swartzii* resulted in dissimilar survival over the subsequent year. Those holdfasts that had 75 % of the holdfast removed experienced significantly higher mortality (mean and 95 % credible intervals; 60 [44, 81] %) compared to all other levels of damage (half: 26 [6.1, 44] %, quarter: 7 [− 15, 25] %, control: 20 [1, 40] %; Fig. 4.5c; Appendix C) over 12 months. All surviving holdfasts were, on average, 40-60 % larger than their initial pre-damage size, with no significant difference in the diameter of surviving *S. swartzii* holdfasts among treatments (Fig. 4.5a; Appendix C). There was very weak evidence of a difference between the height of the control *S. swartzii* (mean and 95 % credible intervals; 56 [18, 97] cm) and the *S. swartzii* that had 75 % of the holdfast removed (89 [50, 128] cm), but no differences between any other treatments (Fig. 4.5b; Appendix C).

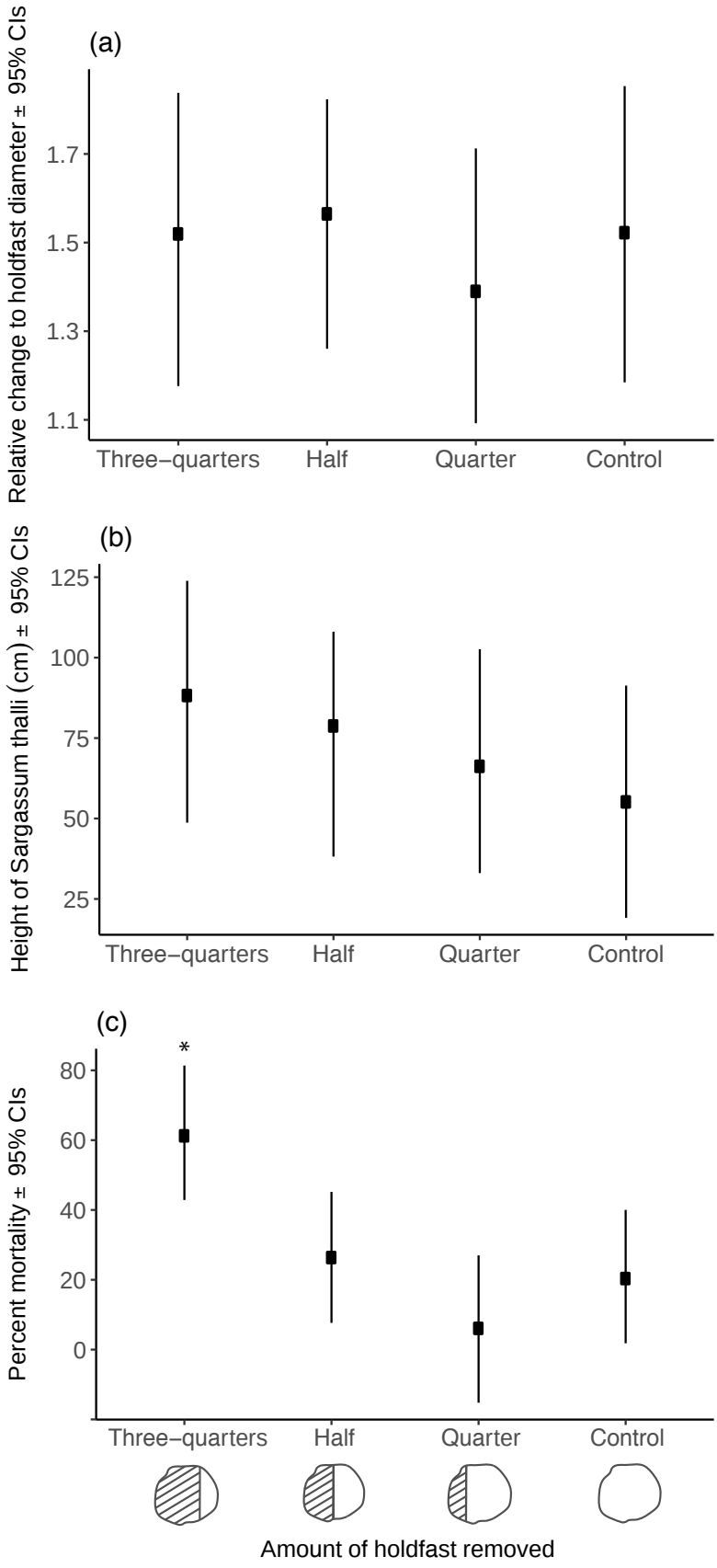

Figure 4.5: (a) Relative change to holdfast diameter of surviving holdfasts 1 year after damage was inflicted ± 95 % credible intervals. The initial size of the holdfasts (before any damage was inflicted) is compared to the final size of holdfasts (1 year post-damage). A relative change of 1.5 would indicate that

the holdfast has increased in size by 50 %; (b) Height of *Sargassum swartzii* thalli (cm) ± 95 % CIs 1 year after damage was inflicted on holdfasts; (c) Percent mortality of *S. swartzii* holdfasts 1 year after damage was inflicted ± 95 % CIs. Asterisk indicates significant difference

4.4 Discussion

Despite widespread recognition that herbivory is essential to the effective functioning of coral reef ecosystems, by limiting the areal extent and biomass of macroalgae (Hay 1981, Bellwood et al. 2004, Graham et al. 2013), the removal of macroalgal holdfasts by herbivores has been largely overlooked. Our results show that while initial removal of *S. swartzii* blades was rapid, the subsequent removal of the stipes and holdfasts was negligible; only one of 53 holdfasts was removed during the 24-day deployment. Removal of the leafy *Sargassum* biomass was largely attributed to feeding by *Naso unicornis* and *Siganus doliatus*, as reported in previous studies (Hoey and Bellwood 2009, 2010a, Bennett and Bellwood 2011, Michael et al. 2013, Chong-Seng et al. 2014). Despite high grazing on many of the exposed rocks, feeding scars were concentrated in the areas free of holdfasts. Critically, low levels of damage had no effect on survival of *S. swartzii*, and 40 % of thalli regrew after 75 % of their holdfast had been removed. Further, damage inflicted on holdfasts had a limited effect on the height of regenerated thalli after one year. Collectively, these results suggest that herbivorous fishes appear to avoid holdfasts, at least for *S. swartzii*, and that holdfasts of this species are extremely resilient to physical damage, which has important consequences for our understanding of how *Sargassum* will respond to disturbance and herbivory.

This study demonstrates the remarkable capacity of *S. swartzii* to regenerate from holdfasts that have had up to three-quarters of their area removed from the substratum. Temperate phaeophytes have been reported to have a similar capacity to

regenerate from small pieces of holdfast (McCook and Chapman 1992, Westermeier et al. 2013). In the present study, the diameter of *S. swartzii* holdfasts and height of the thallus did not substantially differ across treatments one year after damage was inflicted. However, mortality increased when three-quarters of the holdfast was removed from the substratum (60 % mortality) when compared to undamaged controls, and half and quarter-removed treatments (7-26 % mortality). Gorham and Lewey (1984) suggest that the spring growth of *Sargassum muticum* is not predominantly supported by stored polysaccharide reserves in the holdfast, although stores of nitrogen within the holdfast were observed to deplete during this rapid growth phase suggesting nitrogen may somewhat limit the capacity for regeneration. Whilst the mechanisms supporting the regrowth of *Sargassum* from small pieces of holdfast are unclear, this high mortality could be due to a weakening of the holdfasts' attachment to the benthos after damage (Westermeier et al. 2013), or having too few resources to successfully regenerate, as a holdfast's energetic resources are likely to be finite (Gomez and Westermeier 1991). Notably, in the 75 % removed treatment, the original point of stipe growth was removed. It is unknown if having this point of growth removed affected *S. swartzii*'s capacity for regrowth. Nevertheless, this study demonstrates that herbivores must remove over a certain threshold amount (here, 75 %) of the holdfast before the regenerative capacity of *S. swartzii* is reduced. Holdfasts are, therefore, likely to be highly resilient to grazing.

Observed differences in rates of feeding among the components of *Sargassum* may be related to the nutritional composition of those components. Browsing fishes, predominantly *Naso unicornis* and *Siganus doliatus,* quickly consumed the blades and fleshy upper portions of the thallus, as has been reported in several previous studies (Hoey and Bellwood 2009, 2010a, Bennett and Bellwood 2011, Michael et al. 2013,

Chong-Seng et al. 2014). However, the stipes and holdfasts were not readily consumed and many remained after 24-days of exposure to herbivores. Differences in secondary metabolites (phenolics) among tissues are unlikely to explain observed differences in herbivory; Steinberg et al. (1991) demonstrated that rates of herbivory by tropical fishes were not influenced by the amount of phenolics in different species of *Sargassum*. However, the stipes of *S. swartzii* contain approximately 40 % less nitrogen than the blades and holdfasts, which has also been reported in other phaeophytes (Gevaert et al. 2001). This nutritional difference may explain why the stipes were not consumed at the same rate as blades (Diaz-Pulido and McCook 2003), which were removed within the first two days of deployment. Although measurements of physical toughness were not performed in the present study, the physical toughness of *Sargassum* is known to differ among components, with holdfasts being the toughest component followed by stipes (Taylor et al. 2002). This may help explain why all holdfasts except one were left intact despite containing a similar amount of nitrogen as blades.

Only a single holdfast (out of 53 holdfasts) was removed and none of the surviving holdfasts showed any significant signs of damage or change in size by the conclusion of the experiment. The fish species that predominantly grazed on the rocks (i.e., the detritivore *Ctenochaetus striatus,* the algal cropping *Acanthurus nigrofuscus* and *Siganus doliatus* and the browsing *Naso unicornis)* are unlikely to have the jaw morphology or feeding mode required to remove holdfasts from the substratum (Purcell and Bellwood 1993, Konow et al. 2008, Fishelson and Delarea 2014, Tebbett et al. 2017). Although *N. unicornis* consumes leathery brown macroalgae, its jaw and tooth morphology facilitates biting tough algae rather than scraping it off the benthos (as in the case of holdfast removal; Fishelson and Delarea 2014). Indeed, unlike browsing

fishes such as *N. unicornis*, most fishes with the ability to remove holdfasts from the substratum (i.e., parrotfishes) generally do not target or consume leathery brown macroalgae, instead gaining the majority of their nutrition from endolithic or epilithic phototrophs, mainly cyanobacteria, found on or within ingested materials (Clements and Choat 1995, Choat et al. 2004, Clements et al. 2016). Their contribution to holdfast removal is, therefore, likely to be limited.

Despite the apparent lack of herbivory of *Sargassum* holdfasts in the present study, the reversal of a macroalgal regime shift has occurred in a number of locations. Bellwood et al. (2006b) monitored the reversal of an experimentally-induced 'regime shift' dominated by *Sargassum* on an inshore reef of the GBR. Within two months of cage removal, experimental and control (adjacent, non-caged) plots were indistinguishable. In Fiji, the implementation of marine protected areas on reefs dominated by *Sargassum* and other brown macroalgae led to increased coral cover and herbivorous fish biomass inside reserves (Rasher et al. 2013). Furthermore, introducing native sea urchins to reefs manually cleared of invasive macroalgae helped prevent the return of the macroalgae in Kane'ohe Bay, Hawai'i (Conklin and Smith 2005, Goreau et al. 2008, Battista et al. 2016). These studies demonstrate that high rates of herbivory can return an area dominated by macroalgae back to coral dominance (Bellwood et al. 2006b, Rasher et al. 2013). Nonetheless, high browsing pressure that inhibits successful regrowth of macroalgae from the holdfast may be sufficient to cause mortality of the *Sargassum* without direct removal; Gomez and Westermeier (1991) demonstrate that sustained frond removal in the red alga *Iridaea laminarioides* reduced the ability of the holdfast to produce fronds after five months, attributed to the depletion of energetic reserves in the holdfast. If *Sargassum* responds to sustained frond removal in a similar way, perpetual browsing of emergent regrowth may be the most likely mechanism by

which regime shifts to *Sargassum* dominance can be reversed in areas without high numbers of sea urchins.

The capacity of *Sargassum* to regenerate from damaged holdfasts, coupled with the low rate of herbivory on holdfasts, may contribute to the stability of macroalgal-dominated states on coral reefs. The findings of this study suggest that recovery of regime-shifted reefs may only reliably occur with sustained high rates of herbivory by certain browsing fishes that can prevent thalli from successfully regenerating from holdfasts, eventually causing mortality of the whole individual. The preferential consumption of the blades and stipes of the *Sargassum*, along with any associated reproductive structures, may decrease the reproductive capacity of *Sargassum*, as has been shown for temperate macroalgae (Poore et al. 2014, O'Brien and Scheibling 2016), further reinforcing the importance of browsing by fishes such as *Naso unicornis* to the reversal of macroalgal-dominated states. Clearly, further research is required to determine if sustained browsing can cause mortality of *Sargassum* without direct removal of the holdfast, or if there is a threshold of herbivory where holdfasts are damaged by incidental herbivory, preventing the *Sargassum* from regenerating. Nonetheless, this research advances our understanding of macroalgae-dominated reefs and provides further insight into why such states are often so resistant to a return to coral dominance.

Chapter 5: Presence of macroalgal propagules (*Sargassum swartzii)* decreases grazing rates on a coral reef[4]

5.1 Introduction

Herbivory is a key process shaping the biomass, productivity, and composition of primary producer communities across a range of ecosystems, including savannas, woodlands, rocky shores and coral reefs (Lubchenco and Gaines 1981, Hay et al. 1983, McNaughton 1984, Gill and Beardall 2001). While the nature of herbivory and its importance relative to other processes varies among ecosystems, areas of high grazing intensity are typically characterised by a low standing biomass of highly productive herbaceous vegetation, a 'grazing lawn' (McNaughton 1984, Hempson et al. 2015). Within these systems, marked reductions in grazing intensity can lead to shifts to plant communities characterised by a high standing biomass of larger, less productive and less palatable woody vegetation (Anderies et al. 2002, Folke et al. 2004, Hempson et al. 2015). Intense feeding by grazing organisms is thought to maintain productive grazing lawns and prevent shifts to woody vegetation through the incidental consumption of the seedlings of woody species growing within the lawn (McNaughton 1984, Olff et al. 1999, Uytvanck et al. 2008).

Within coral reef ecosystems, shifts between highly productive algal turf assemblages and stands of tall, fleshy, typically brown, macroalgae have been linked to changes in herbivory (Done 1992, Hughes et al. 2007). On reefs with intact herbivore populations, algal assemblages are typically dominated by short, highly productive

[4] Loffler, Z, Graba-Landry, A, Hoey, A.S. Presence of macroalgal propagules (*Sargassum swartzii)* decreases grazing rates on a coral reef. In prep.

algal turfs, the Epilithic Algal Matrix (EAM, a conglomerate of filamentous algae, macroalgal propagules, detritus, invertebrates, microbes and sediment; Wilson et al. (2003)), with over 90 % of daily algal production consumed by grazing fishes and invertebrates (Hatcher and Larkum 1983, Polunin and Klumpp 1992). However, if rates of herbivory decrease (e.g., overfishing) and/or rates of algal production increase (e.g., eutrophication and/or increases in algal cover following coral mortality), algal production may exceed consumption, releasing macroalgal propagules within the EAM from top-down control and potentially leading to a shift to tall, fleshy macroalgae (Done 1992, Hughes et al. 2007). Once established, such shifts have proven difficult to reverse as the macroalgae that tend to dominate such regimes (e.g., *Sargassum*) are unpalatable to the majority of herbivores (Bellwood et al. 2006b), and a series of positive feedbacks reinforce the presence and expansion of macroalgal populations and/or suppress the recovery of coral populations (Mumby and Steneck 2008, van de Leemput et al. 2016, Clements et al. 2018).

Clearly, preventing, rather than reversing, a regime shift is more desirable. To date, however, the vast majority of research on the susceptibility of macroalgae to herbivory has focused on the consumption of adult algal biomass (McCook 1997, Hoey and Bellwood 2009, Vergés et al. 2011, Chong-Seng et al. 2014); few studies have investigated the susceptibility of propagules to grazers (Diaz-Pulido and McCook 2003). Indeed, the potential removal of macroalgal propagules within the EAM by grazing fishes has largely been inferred from changes in algal communities following reductions in, or exclusion of herbivores, rather than from empirical investigations (but see Diaz-Pulido and McCook (2003)). It is unknown if the presence of macroalgal propagules within the EAM alters the feeding behaviour of grazing fishes, just as terrestrial grazers avoid areas containing non-preferred species (Olff et al. 1999, Smit et

al. 2006). This study, therefore, aimed to investigate if the presence of *Sargassum* propagules (a common macroalga on degraded coral reefs (Hughes 1994, Rasher et al. 2013, Graham et al. 2015)), within the EAM affects the feeding behaviour of grazing fishes.

5.2 Materials and Methods

5.2.1 Study sites

This study was conducted from October to December 2017 at Lizard Island in the northern Great Barrier Reef (GBR), Australia (14°40'S, 145°28'E; Appendix D). Lizard Island is a high continental island approximately 40 km from the Queensland coast. Two sites within each of two habitats, the reef crest and reef flat, were chosen on the south-east, or exposed, aspect of the reef surrounding the Lizard Island lagoon (Appendix D). The reef flat sites were characterised by low structural complexity and fish biomass, and a water depth of 0.5 m to 2.5 m. The reef crest sites had higher structural complexity and fish biomass, with depths of 1.5 to 3.5 m, depending on tidal state. To determine if the presence of *Sargassum* propagules within the EAM affected grazing rates, paired experimental tiles (one with EAM containing *Sargassum* propagules, the other with EAM without *Sargassum* propagules) were exposed to local herbivorous fish assemblages for six days at each of two reef crest and reef flat sites in early December 2017.

5.2.2 Cultivation of EAM and propagules on tiles

Thirty-eight terracotta settlement tiles (110 x 110 x 10 mm) were placed on the bottom of each of two 1000 L outdoor aquaria with supplemental aeration and flow through seawater to seed tiles with a bacterial film and turf algal community. The two aquaria

were positioned side by side and received fresh seawater from the same source. Each tile was marked with a unique label on one edge using permanent marker. After 32 h, all tiles within one aquarium were seeded with propagules of *Sargassum swartzii*.

Fifty adult, reproductive *S. swartzii* thalli were collected by hand from the inshore reefs of the Turtle Group (14°43'S, 145°12'E), approximately 28 km west of Lizard Island and 11 km from the mainland. These thalli were transported back to Lizard Island within 3 h of collection in 80 L plastic aquaria (L x W X H: 60 x 37 x 38 cm) filled with seawater. Within 5 h of collection, the *S. swartzii* thalli were stressed to stimulate propagule release by placing them in an 80 L aquarium filled with cold seawater (9 °C) for 10 minutes (following Carl et al. (2014)). Thalli were then transferred to one of the 1000 L aquaria containing settlement tiles at ambient (26 °C) seawater temperature with supplemental aeration. The reproductive *Sargassum* were agitated by hand twice per day to further encourage release of the propagules, and left with supplemental aeration for three days, during which time the flow-through seawater to both aquaria was turned off. After this time, the adult *Sargassum* was removed and the water in the aquarium drained and filtered through 20-micron plankton mesh to prevent any unattached propagules being released out onto the reef. Flow-through seawater was subsequently turned on for both aquaria.

The tiles were cultured in these aquaria with flow-through seawater and supplemental aeration for ten days, to allow the *Sargassum* propagules time to firmly attach to the tiles (Fletcher and Callow 1992). All 76 tiles were then translocated to a sheltered site within the Lizard Island lagoon (Appendix D) and placed within mesh cages (32 x 15 x 4 cm, 5mm plastic mesh; two tiles per cage) for 21 days to allow EAM to establish in the absence of herbivory. After 21 days, the tiles were collected, transported back to the research station in aquaria filled with seawater, and placed into

tanks with flow-through seawater for quantification of *Sargassum* propagule density. The density of propagules on the 38 tiles with settled propagules was quantified within 24 h of collection using 14 replicate 1 x 1 cm quadrats placed haphazardly on the upper surface of each tile. Propagules were ~2-3 mm tall. There was no difference in the height of turf algae between EAM only and EAM with propagules tiles (Appendix D). Hereafter, tiles with EAM only will be referred to as 'EAM only' tiles, and tiles with *S. swartzii* propagules within the EAM will be termed 'EAM with propagules' tiles.

5.2.3 Herbivore exposure

To determine if the presence of *Sargassum* propagules in the EAM affected the feeding rate of grazing fishes, and if any feeding on the tiles affected the density of *Sargassum* propagules, tiles were paired (one EAM only and one EAM with propagules tile) and deployed on the reef for six days.

Tiles were deployed on the reef crest and flat using stainless steel plates mounted on clay bricks (L x W x H: 250 x 80 x 50 mm). A bolt attached to each steel plate was passed through a hole in the centre of each tile and a wing nut used to secure the tile to the plate. Each base plate was attached with cable ties threaded through the holes in the base plate to clay bricks. Two base plates were attached to each brick, which allowed the pair of tiles (one with EAM with propagules, one with EAM only) to be secured adjacent to one another. Using this method, the gap between all paired tiles was no greater than 1-2 cm. Tiles attached to bricks in this way sat approximately 10 cm above the benthos. Ten bricks with attached paired tiles were placed at each site except one reef flat site where only eight pairs were deployed. Half of the tile pairs were left exposed to local fish assemblages, and half were placed within exclusion cages (L x W x H: 300 x 150 x 40 mm; 5mm mesh) to control for any effects of

handling and rates of propagule mortality in the absence of herbivory. The size of this mesh meant that extremely small fishes (~10mm long, 1-2mm wide) were able to enter the cages, however, their contribution to any propagule mortality would have been negligible, as propagules were ~2-3 mm tall. Smaller mesh may have quickly fouled and shaded the propagules within the cage, potentially causing propagule mortality. Each tile pair within a site were separated by at least 3 m. After six days, the tiles were collected, removed from the base plates and placed on a steel bar with plastic spacers between each tile and transported back to the research station in plastic aquaria filled with seawater. The density of *Sargassum* propagules on each tile was quantified within 24 h of collection, as described above.

At each site, feeding on four of the exposed tile pairs was recorded using remote underwater video cameras (Go Pro HERO3 and HERO4). A GoPro camera attached to a small dive weight was placed adjacent (within 40 cm) to each of the four tile pairs at each site (16 cameras per day) between 08:00 and 09:00 and recorded continuously for three hours. This process was repeated for five days with the same tile pairs being recorded throughout the experiment (i.e., one pair at each site that had five exposed pairs was never videoed). The entire video footage (~240 h) was viewed and for each individual fish observed taking bites on the tile, the species of fish, number of bites, total length of the fish and location of bites (i.e., EAM only vs EAM with propagules) was recorded. Length of the fish was estimated to the nearest centimetre by comparing size relative to the known tile length (11cm). For those fishes that were too small (or the video resolution too coarse) to accurately identify to species, they were recorded to the lowest taxonomic level possible (usually genus).

5.2.4 Statistical analysis

All statistical analyses were conducted in R version 3.3.2 (R Development Core Team 2016) and Bayesian models fitted in STAN with Markov Chain Monte Carlo sampling using the rstanarm package version 2.13.1 (Stan Development Team 2016a). Broom (version 0.4.4; Robinson 2017) and CODA (version 0.19.1; Plummer et al. 2006) packages were used to summarise the model outputs using highest posterior density intervals (probability level = 0.95). Plots were produced using *ggplot2* version 2.2.1 (Wickham and Chang 2008).

5.2.4.1 Overall herbivore pressure

To determine if herbivory differed between EAM only and EAM with propagules tiles, an interactive generalised linear mixed effects model using a negative binomial error distribution with a log link transformation was used. The bites of all species biting on a given tile on a given day were summed, and this was included as the response variable. A negative binomial error distribution was used because the model fitted with Poisson error distribution showed evidence of overdispersion. The model included the fixed effects of substrate (EAM only or EAM with propagules), habitat and site, with an interaction term included for the relationship between habitat and treatment. Including site in the interaction did not improve model fit, determined using leave-one-out cross-validation (Vehtari et al. 2018), therefore site was included as an additive fixed effect. Tile nested within day was included as a random factor, to account for the non-independence of days, and EAM only and EAM with propagules tiles being presented adjacent to one another. The model used weakly informative priors on intercept (normal(0,5)) and slope coefficients (normal(0,5)) and error standard deviation (Cauchy(0,5)) with 5000 iterations, a warmup of 2500, three chains and a thinning factor of three. Planned contrasts were also used to compare the difference in bites

between EAM only and EAM with propagules tiles in each habitat and site combination.

5.2.4.2 Bite rate of individual species

To determine if individual fish species displayed different bite rates on EAM only vs. EAM with propagules tiles, species that took bites on at least three tile pairs each day were subset from the dataset and analysed individually. If bites were taken on fewer than three tile pairs in one day, that day was not included in the analysis. Some species took a large number of bites on only one tile pair, and therefore were not eligible for individual analysis due to the lack of spatial replication. Fishes of the genus *Pomacentrus* were pooled for analyses. Generalised linear mixed effects models were used to examine if the bite count of *Ecsenius stictus, Pomacentrus* spp. or *Ctenochaetus striatus* differed between EAM only and EAM with propagules tiles. The models were interactive and used a negative binomial error distribution with a log link transformation as the models displayed evidence of overdispersion when fitted with a Poisson distribution. Bite count was included as the response variable, with substrate (either EAM only or EAM with propagules) and habitat (reef flat or reef crest) included as fixed factors. *Ctenochaetus striatus* only took bites on tiles on the reef crest, therefore habitat was not included in the model. Tile nested within day was included as a random factor. Weakly informative priors were used on intercept (normal(0,3)) and slope coefficients (normal(0,3)) and error standard deviation (Cauchy(0,4)). 6000 iterations were used, with a warmup of 3000, a thinning factor of four and three chains.

5.2.4.3 Propagule survival

To examine the survival of propagules when exposed to herbivory, a generalised linear model was used, fitted in a Bayesian framework using the function 'stan_glm' using a Gaussian error distribution with an identity link transformation. The proportion of propagules remaining on each tile after six days on the reef was used as the response variable, and was log transformed prior to analysis to meet model assumptions. The model included the fixed effects of habitat, treatment and site, with an interaction term included for the relationship between habitat and treatment. Including site in the interaction did not improve model fit, determined using leave-one-out cross-validation (Vehtari et al. 2018), therefore site was included as an additive fixed effect. Weakly informative priors were used on slope coefficients (normal(0,3)), intercept coefficients (normal(0,3)) and the error standard deviation (Cauchy(0,5)), with 5000 iterations, a warmup of 2500, a thinning factor of five and three chains. Planned contrasts were used to compare the survival of propagules on caged vs. exposed tiles between habitats and sites using 95 % higher posterior density intervals.

For all models, diagnostic plots were examined to ensure chains were well mixed and had converged on a stable posterior distribution, that there was no evidence of autocorrelation and that priors were sufficiently wider than posterior values. All values of Rhat were less than 1.05 and sampling chain estimates corresponded to the observed data.

5.3 Results

5.3.1 Fish bites on tiles

Analysis of the rate of herbivory between EAM only and EAM with propagules tiles revealed marked differences in the bite rate between treatments. The overall bite rate was higher on EAM only tiles than EAM with propagules tiles, averaging (mean [95%

Credible Intervals]) 55.93 [4.10, 130.3] and 35.64 [3.00, 81.89] bites hr^{-1}, respectively (Fig. 5.1). Although bite rates were significantly higher on the reef crest (80.17 [6.4, 185.90] bites hr^{-1}) than reef flat (11.40 [0.70, 26.30] bites hr^{-1}), planned contrasts showed that the higher bite rate on EAM only tiles was consistent across both sites and in both habitats (Appendix D).

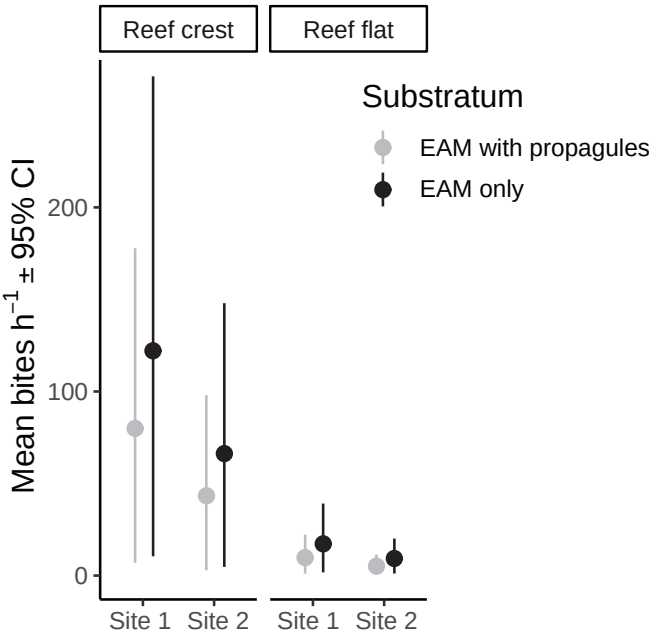

Figure 5.1: Average number of bites summed across all fish species on each substrate (EAM only vs. EAM with propagules) in each habitat (reef flat or reef crest) and site (Site 1 or Site 2) combination, using means ± 95% Credible Intervals

Feeding on the tiles was dominated by *Escenius stictus* (f. Blenniidae), which accounted for 85% of total bites. *Pomacentrus* spp. (f. Pomacentridae), and *Ctenochaetus striatus* (f. Acanthuridae) each took 1 % of total bites. Other species with a higher percentage of total bites took bites on tiles with limited spatial and/or temporal replication, and therefore could not be formally analysed (see Appendix D for table of all species with their corresponding bite count). Both *E. stictus* and *Pomacentrus* spp. took significantly more bites on EAM only tiles than EAM with propagules tiles on

both the reef crest (*E. stictus*: 40.68 [0.46, 105.90] vs. 24.41 [0.23, 62.78] bites hr^{-1}; *Pomacentrus* spp.: 0.24 [0.02, 0.61] vs 0.09 [0.01, 0.23] bites hr^{-1}) and reef flat (*E. stictus*: 8.56 [0.05, 23.23] vs 4.42 [0.03, 12.31] bites hr^{-1}; *Pomacentrus* spp.: 0.65 [0.03, 1.58] vs 0.25 [0.02, 0.64] bites hr^{-1}; Figs. 5.2a, b). There was no evidence of a difference in bite rate for *Ctenochaetus striatus,* who took a similar number of bites on both tiles (EAM only: 1.18 [0.15, 2.46], EAM with propagules: 1.04 [0.12, 2.17] bites hr^{-1}, respectively Fig. 5.2c). Notably, none of these fish species took significantly more bites on EAM with propagules tiles than EAM only tiles.

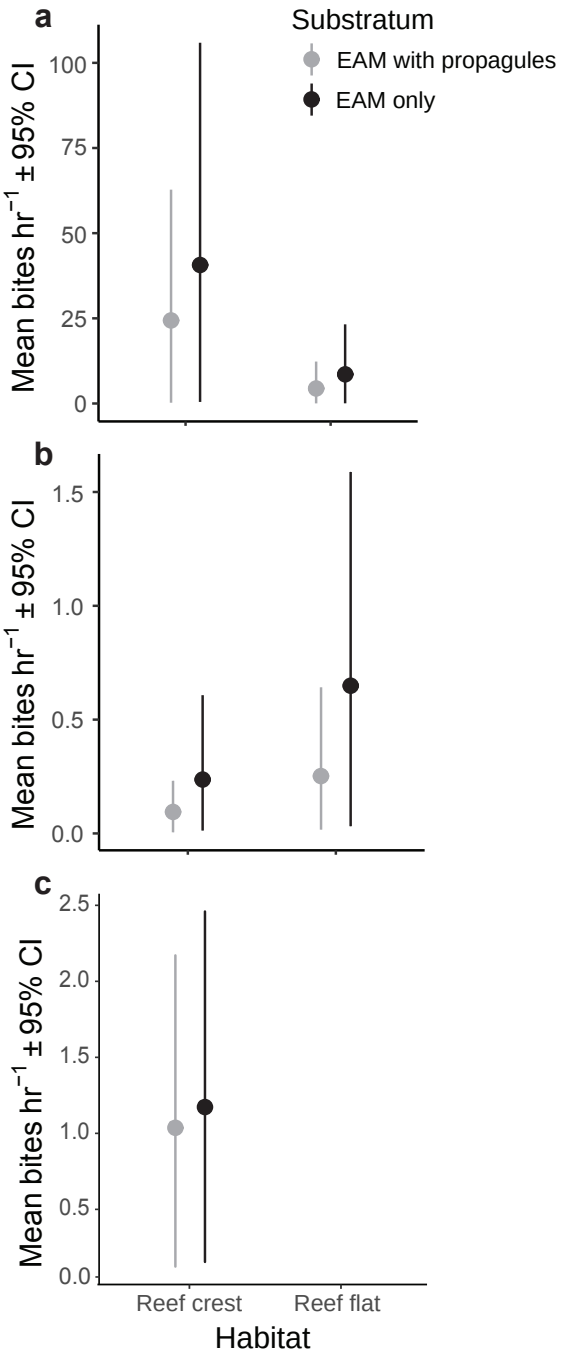

Figure 5.2: Mean bites per hour by (a) *Ecsenius stictus*, (b) *Pomacentrus* spp. and (c) *Ctenochaetus striatus* on each substrate (EAM only vs. EAM with propagules) in each habitat (reef flat or reef crest), using means ± 95% Credible Intervals. Note: *Ctenochaetus striatus* only took bites on tiles on the reef crest.

Propagule survival

There was a significant decline in the density of propagules on EAM with propagules

tiles exposed to local herbivore assemblages compared to those within exclusion cages (Fig. 5.3). The survival of propagules on caged vs. exposed tiles on the reef crest was (mean [95% Credible Intervals]) 0.95 [0.77, 1.14] vs. 0.45 [0.36, 0.54], respectively. The difference between caged and exposed tiles was smaller on the reef flat, with survival of propagules on caged tiles averaging 0.91 [0.73, 1.10] compared to 0.69 [0.56, 0.83] on tiles exposed to local fish assemblages.

Planned contrasts revealed that that there was a significant difference in survival between caged and exposed tiles on the reef crest at both sites (Site 1: 0.47 [0.31, 0.65]; Site 2: 0.53 [0.33, 0.73]). There was weaker evidence of a difference on the reef flat, with 95 % higher posterior density intervals very close to zero at both Site 1 (0.21 [0.01, 0.41]) and Site 2 (0.24 [0.01, 0.46]; Appendix D).

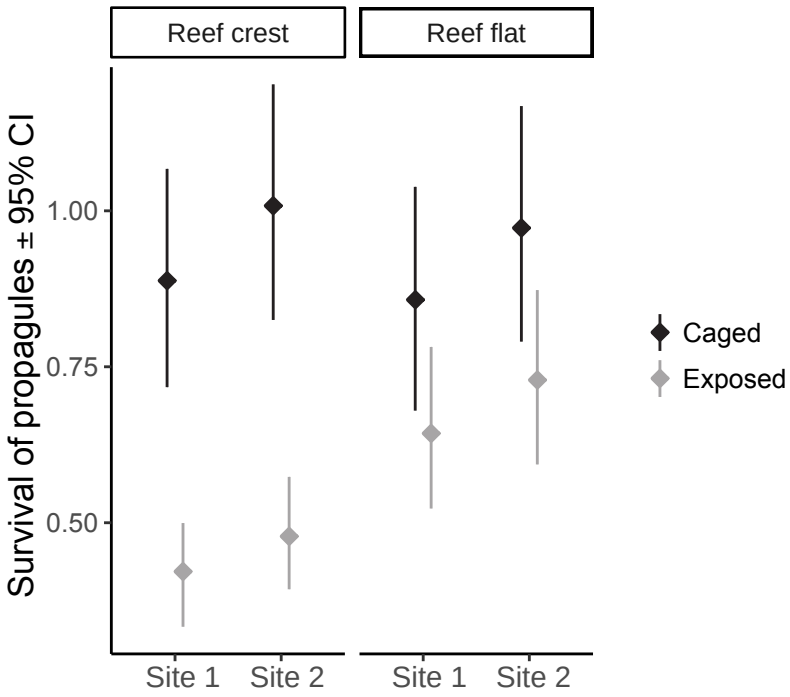

Figure 5.3: Proportion survival of *S. swartzii* propagules on tiles deployed on the reef for six days alongside EAM only tiles in each habitat, site and treatment (caged or exposed to herbivore assemblages) combination. Values represent means ± 95% Credible Intervals

5.4 Discussion

Grazing herbivores are often assumed to be critical in preventing shifts from highly productive 'grazing lawns' to a higher biomass of less productive vegetation through the incidental grazing of seedlings of woody plants or propagules of fleshy macroalgae (McNaughton 1984, Hempson et al. 2015). However, the capacity for grazers to remove these propagules and the influence of these propagules on herbivore feeding has not been investigated. Our results show that the overall rate of herbivory was 36 % lower on EAM with propagules than EAM only tiles, suggesting that fishes could detect the presence of *Sargassum* propagules and reduced their feeding on algal turfs where the propagules were abundant. Importantly, none of the fishes individually analysed showed a significantly higher bite rate on surfaces with *Sargassum* propagules present versus those where they were absent. Despite the lower grazing pressure on surfaces containing *Sargassum* propagules, grazing led to a 39 % reduction in the survival of *Sargassum* propagules over six days on the reef. The lower grazing rates on EAM containing *Sargassum* propagules may have significant implications for the replenishment and spread of *Sargassum* communities on degraded and inshore coral reefs.

Critically, this study found that the presence of *S. swartzii* propagules within the EAM caused a significant decrease in grazing rates, suggesting that grazing fishes were able to detect the presence of *Sargassum* propagules within the EAM. When rates of herbivory are high, grazers are assumed to non-selectively consume seedlings/propagules while maintaining closely cropped 'lawns' (Choat 1982, McNaughton 1984, Mumby 2006). Our results did not completely support this theory, as rates of grazing were affected by the presence of *Sargassum* propagules within the EAM. Grazing fishes on coral reefs may adjust their feeding rates in response to the composition of the EAM, feeding less on areas containing non-preferred elements. The

apparent avoidance of EAM containing *Sargassum* propagules may be related to chemical and/or physical defences or the nutritional content of the propagules; previous studies have suggested that herbivore preferences between algal species are largely determined by the properties of the primary producers they target (Hay and Fenical 1988, Hanley et al. 2007, Rasher et al. 2013). However, unlike adults, *S. swartzii* propagules do not have a tough morphology, and recruits (<1 cm in height) of the tropical congener *Sargassum mangarevense* produce 75 % fewer phenolic compounds than adults (Stiger et al. 2004). It is unknown if the presence of any phenolic compounds within the *S. swartzii* propagules could have caused the lower grazing rates seen in the present study. Nevertheless, just as terrestrial ungulate preferences between plant species and associated changes in grazing rates can create a mosaic of tall and short grasslands with differing species compositions and productivities (McNaughton 1984, McNaughton et al. 1997, Augustine and McNaughton 1998), the discrepancy in grazing rates on areas with and without propagules could contribute to a similar mosaic of short, productive EAM and less productive macroalgal stands on coral reefs.

Previous research into grazing of macroalgal propagules and its consequences for coral reefs is limited. However, research from temperate rocky shores has reported that grazers avoid consuming brown algal germlings in favour of green algal germlings (attributed to differences in anti-herbivore compounds among the different algal species), promoting the survival of the brown alga and inducing a shift from susceptible green to more grazer-resistant brown algal germlings (Hay and Fenical 1988, Lotze et al. 2000, 2001). The temperate blenny *Scartichthys viridis* has also been shown to selectively graze on green algae and avoid less palatable brown species, with the macroalgal assemblage dominated by brown and red species where these blennies are abundant (Ojeda and Alejandro 1999). Lower grazing rates on areas of the EAM

containing non-preferred *Sargassum* propagules could, therefore, promote the survival of *Sargassum* on coral reefs, as has been reported for brown macroalgae on temperate rocky shores.

Although there was a significant decrease in the density of propagules on tiles exposed to herbivores, it is largely unknown how herbivory at this early post-settlement stage may affect the probability of survival to adulthood, or indeed to a size refuge from grazing fishes. However, *Sargassum* propagules on tiles placed on the reef crest and flat within cages for 16 days showed an average change in height from 0.2 to 3.8 mm, an increase of 0.23 mm day^{-1} (Loffler, unpub. data). If linear growth is assumed, it would take ~44 days for propagules to reach 1 cm, the defined height of change from recruit to juvenile (Stiger et al. 2004), and a possible size refuge from blennies. Furthermore, given that the propagules exposed to herbivory showed a survival of 45 % on the reef crest and 69 % on the reef flat in six days in the present study, if the rate of mortality is assumed to be constant, 0.37 % of propagules on the reef crest and 7.5 % on the reef flat would survive to reach 1 cm height. This difference in survival between habitats may partly explain why *Sargassum* is common on reef flats of the GBR but rare on the reef crest (McCook 1997). Similar high levels of propagule mortality have been reported by temperate studies examining the recruitment of *Sargassum* propagules, with a reported rate of recruit mortality of >99 % after one year (Kendrick and Walker 1994). It is likely that mortality from grazers during this early post-settlement period will greatly affect the rate of survival to adulthood, as rates of mortality were low on caged tiles in the present study. However, these mortality estimates do not consider any processes operating in or near *Sargassum* beds that may enhance the survival of recruits (Dell et al. 2016).

Contrary to expectations from previous research (Done 1992, Diaz-Pulido and McCook 2003, Bellwood et al. 2004), large-bodied grazers such as surgeonfish, rabbitfish and parrotfish were not the dominant grazers on the tiles. The lack of bites by large bodied grazers may be due to the high cover of natural EAM on the reef following two cyclones and coral bleaching events occurring in the previous five years (Chapter 2). In this location, tiles may have presented a relatively less attractive resource than if presented on other coral reefs with higher coral cover. Nevertheless, these findings highlight that the contribution of cryptobenthic reef fishes such as blennies to consumption of algal materials on coral reefs may be greater than previously assumed, as cryptobenthic fishes likely have a high capacity for consumption of EAM materials due to their high biomass, high metabolism and fast growth rates (Depczynski and Bellwood 2003, Brandl et al. 2018).

The reduced grazing on EAM containing *Sargassum* propagules is a potential positive feedback that may facilitate the expansion of *Sargassum* beds and adds to a growing number of studies that have identified positive feedbacks operating within *Sargassum*-dominated areas. These include enhanced growth of conspecifics in *Sargassum* beds (Dell et al. 2016), the reluctance of herbivores to enter dense stands of *Sargassum* (Hoey and Bellwood 2011), the inhibition of coral growth and recruitment (Hughes et al. 2007, Webster et al. 2015, Clements et al. 2018) and vectoring of coral disease (Nugues et al. 2004). In the present study, the presence of *Sargassum* propagules caused a decrease in the grazing rate despite the density of propagules being relatively low (10 propagules cm^{-2}) compared to observed natural densities, which can reach 800 propagules cm^{-2} in temperate *Sargassum* beds (Kendrick and Walker 1994). *In situ*, densities of settled propagules are likely to be highest directly adjacent to adult *Sargassum*, as *Sargassum* propagules generally settle within one metre of the parent, at

least on temperate reefs (Kendrick and Walker 1991, 1995). The reluctance of grazing fishes to graze areas with high densities of *Sargassum* propagules may promote the expansion of *Sargassum* beds through enhanced propagule survival close to conspecifics (Dell et al. 2016), although see (Bennett and Wernberg 2014).

In summary, our findings demonstrate that the presence of *Sargassum* propagules within the EAM alters the feeding behaviour of grazing fishes. Despite the decreased grazing rate on EAM containing propagules, the mortality of *Sargassum* propagules was still high, especially on the reef crest (ca. 55 % in 6 days) compared to the reef flat (ca. 30 % in 6 days). Just as varying rates of grazing across a landscape can create a mosaic of closely cropped lawns interspersed with taller vegetation (McNaughton 1984), the reduced grazing rates on EAM containing *Sargassum* propagules may present a mechanism enhancing the survival of *Sargassum* propagules through lowered levels of herbivory. Processes operating within established macroalgal beds can be complex and self-reinforcing, and the findings of the present study suggest another positive feedback enhancing the persistence and expansion of macroalgal-dominated areas on coral reefs.

Chapter 6: Microhabitats enhance recruitment and survival, but inhibit growth of propagules of the tropical macroalga *Sargassum swartzii*[5]

6.1 Introduction

For organisms with discrete life history stages, processes affecting dispersal, settlement and early post-settlement survival can have a large influence on adult population size (Connell 1985, Vadas et al. 1992). Indeed, for many marine organisms, the first few days following settlement have been identified as a critical period shaping adult populations, as recently-settled individuals are typically small (Vadas et al. 1992, Hunt and Scheibling 1997), undergo a range of physiological changes (McCormick et al. 2002), and are exposed to a diverse suite of demersal predators for the first time (Vadas et al. 1992, Almany and Webster 2006, Scheibling and Robinson 2008). For example, mortality in the first days to weeks after settlement has been estimated to be as high as 58 % for coral recruits (Vermeij and Sandin 2008, Trapon et al. 2013b), up to 75 % for coral reef fishes (Hoey and McCormick 2004, Almany and Webster 2006), greater than 90 % for many marine invertebrates (Gosselin and Qian 1997, Hunt and Scheibling 1997) and up to 99 % for temperate marine algae (Vadas et al. 1992, Kendrick and Walker 1994). Any factors that mediate rates of mortality at this critical life history transition are, therefore, likely to have a large impact on the number of individuals reaching the adult population. Such mediating factors include the size of an individual

[5] Loffler, Z and Hoey, A.S. Microhabitats enhance recruitment and survival, but inhibit growth of propagules of the tropical macroalga *Sargassum swartzii*. In revision for Marine Ecology Progress Series.

(i.e., 'bigger-is-better' hypothesis (Miller et al. 1988, Bailey and Houde 1989)), growth rate (i.e., 'stage duration' hypothesis (Leggett and Deblois 1994)), physiological condition (e.g., Hoey and McCormick 2004), inter- and intra-specific competition (Menge 1976, Bonin et al. 2009), and the structural complexity and suitability of the settlement habitat (Diaz-Pulido et al. 2010, Yadav et al. 2016, Mallela 2018). Of these, structural complexity of the settlement habitat is thought to be a major driver of rates of survival (Tupper and Boutilier 1997, Nozawa 2008, Mallela 2018).

The structural complexity of a habitat (i.e., its three-dimensional structure, composed of living and dead organisms and abiotic substrata) can mediate rates of mortality through the provision of refugia (Crowder and Cooper 1982, Graham and Nash 2013). The value of structural complexity in providing refugia is dependent on the relative size of available refuges: large enough to allow prey to access, but small enough to exclude predators (Menge and Lubchenco 1981). Therefore, small-scale structural complexity, such as small cracks and crevices, may allow recently settled organisms to avoid the predation pressure of adjacent open or exposed surfaces (Menge and Lubchenco 1981, Brandl et al. 2014, Franco et al. 2015).

On coral reefs, early post-settlement mortality is high (>50 %) for both fish and corals (Almany and Webster 2006, Nozawa 2008), and has led to this being viewed as a critical period in the life history of these organisms. Importantly, however, specific microhabitats can enhance the early post-settlement survival of corals and reef fish several-fold, presumably through the provision of refugia (Nozawa 2008, Bonin et al. 2009, Brandl et al. 2014). For example, Nozawa (2008) reported the complete mortality of corals that had settled on exposed surfaces within four months, while up to 12 % of corals that had settled in crevices survived the first year post-settlement. Similarly, the early post-settlement survival of coral reef fishes is also enhanced when fishes settle on

patch reefs with higher structural complexity (Bonin et al. 2009). Whilst the importance of microhabitats to the settlement and survival of corals and fishes has been relatively well-studied (Nozawa 2008, Bonin et al. 2009, Trapon et al. 2013a, Doropoulos et al. 2016), the importance of microhabitats for early life stages of macroalgae has only been inferred (Brandl et al. 2014).

To date, studies investigating spatial and temporal variation in rates of herbivory on coral reef macroalgae have primarily focused on the consumption of adult thalli (Hay 1981, Lewis 1986, Loffler et al. 2015), yet it is often assumed that macroalgal biomass is largely controlled through the grazing of early life stages of macroalgae (Done 1992, Diaz-Pulido and McCook 2003, Bellwood et al. 2004). Spatial and temporal refuges may equally facilitate the early post-settlement survival of macroalgae by providing a refuge from herbivory, potentially allowing propagules to grow to a size more resistant to grazing (Lubchenco 1983, Stiger et al. 2004, Briggs et al. 2018). In this study, therefore, I investigate how reef microtopography (i.e., crevices) influences the recruitment, growth and survival of propagules of the common tropical macroalga *Sargassum swartzii*.

6.2 Materials and Methods

6.2.1 Study organism

Sargassum is a genus of tall (up to 3 m), leathery, brown macroalgae common on many coastal and/or degraded coral reefs (Done 1992, Chong-Seng et al. 2014). *Sargassum* reproduces through the release of tens of thousands of zoospores per plant (Diaz-Pulido and McCook 2003), with mortality of settled propagules in temperate *Sargassum* near absolute (ca. 99.9999 % after one year (Kendrick and Walker 1995)). Any reduction in early post-settlement mortality may, therefore, result in a higher rate of survival to

adulthood (Vadas et al. 1992). The species *Sargassum swartzii* was used to investigate the value of microtopographic refuges for the recruitment and survival of *Sargassum* propagules, as this species occurs in high abundance on inshore reefs in the northern Great Barrier Reef (GBR; Wismer et al. (2009)).

6.2.2 Study sites

This study was conducted between October-November 2017 at Lizard Island, a granitic mid-shelf island in the northern Great Barrier Reef (GBR), Australia (14°40'S, 145°28'E; Appendix E). To examine the effect of microtopography on the recruitment, growth and survival of macroalgae propagules, I settled *Sargassum swartzii* propagules to tiles with regular crevices and exposed these tiles to local herbivore assemblages on the exposed reef flat and reef crest (Appendix E). These two reef zones were selected as they differ in depth, benthic composition, and rates of herbivory. Reef flat zones are generally characterised by lower rates of herbivory, lower structural complexity and a higher abundance of macroalgae (especially on inshore reefs) than reef crest zones (Fox and Bellwood 2007, Hoey and Bellwood 2010a). Depth differs across the two reef zones, with the reef flat experiencing diel tidal changes resulting in water depths between 0.5 m to 2.5 m, and the reef crest experiencing water depths between 1.5 to 3.5 m.

6.2.3 Collection of adult Sargassum swartzii and seeding of propagules

Forty-eight terracotta settlement tiles (110 x 110 x 10 mm), each with four crevices (4 mm wide, 3 mm deep, 110 mm long) spaced evenly across the top surface of the tile (Appendix E), were placed on the bottom of a 1000 L aquarium. After 24 hours, reproductively mature *S. swartzii* were stimulated to release propagules and added to the aquarium.

Fifty adult, reproductively mature *S. swartzii* thalli were collected by hand from the inshore reefs of the Turtle Group (14°43'S, 145°12'E), approximately 11 km west of Lizard Island (Appendix E). Thalli were kept in 80 L plastic aquaria (L x W x H: 60 x 37 x 38 cm) filled with seawater and returned to Lizard Island within 3 h of collection. Thalli were stressed within 5 h of collection using cold-shock to stimulate propagule release. Briefly, thalli were placed in an 80 L plastic aquaria filled with cold seawater (9 °C) for 10 minutes (following Carl et al. (2014)), and then transferred to the 1000 L aquarium containing the tiles at ambient (26 °C) seawater temperature. The *S. swartzii* thalli were then agitated in the 1000 L aquarium by hand twice per day to further encourage release of the propagules and were left in this aquarium with static water and supplemental aeration for three days. After three days, the adult *S. swartzii* were removed from the tank and the water remaining in the aquarium filtered through 20-micron mesh. The tiles with attached propagules were cultured in the aquarium with supplemental aeration and flow-through seawater for 18 days.

In order to determine if recruitment (i.e., settlement and any mortality during the first 18 days) was higher in crevices than on the upper, exposed microhabitat (i.e., the flat surface of the tiles between crevices; Appendix E) of the tiles, the density of propagules within crevices and on the exposed microhabitat of the tiles was quantified after 18 days by haphazardly placing a quadrat (L x W: 25 x 4 mm; area: 1 cm^2) either over a crevice, matching the width of the quadrat to the width of the crevice (8 quadrats/tile) or on the exposed microhabitat (10 quadrats/tile) of the tile. To determine if there were any differences in the growth of propagules that had settled in the crevices versus the exposed microhabitat of the tiles, the height of ten propagules (per microhabitat per tile) on a subset of six haphazardly chosen tiles were measured to the nearest 0.1 mm with callipers.

6.2.4 Herbivore exposure

To determine the susceptibility of propagules within crevices versus those on adjacent exposed microhabitats to herbivory, tiles seeded with propagules were deployed on the reef for five days. Each tile was secured to the reef by passing a bolt attached to a stainless-steel base plate through a 5 mm hole in the centre of the tile and fastening with a wingnut; push mounts were used to secure the base plate into drilled holes in the reef (following Mundy (2000)). Twelve tiles were deployed at each of two reef crest and two reef flat sites, with at least 3 m between adjacent tiles within a site. Within each site, six tiles were left exposed to local herbivore assemblages, and six tiles were placed within exclusion cages (L x W x H: 150 x 150 x 40 mm; 5 mm square plastic mesh) to control for the effects of handling and translocation. After five days, the tiles were collected, placed onto a stainless-steel bar with 10 mm plastic spacers between each tile to prevent contact between tiles and transported back to the research station in small aquaria with 30 min of collection. Tiles were placed back into the 1000 L aquarium with flow-through seawater and supplemental aeration and the density of propagules within crevices and on the exposed microhabitat of each tile was re-quantified as previously described.

6.2.5 Video observations

At each site, four of the six tiles exposed to herbivores were haphazardly chosen to record feeding activity using stationary underwater video cameras. A small video camera (GoPro HERO3 or HERO4) attached to a dive weight was placed adjacent (30-40 cm) to each of the four selected tiles at each of the four sites (16 cameras per day). Each camera started recording between 08:00-09:00 and recorded continuously for

three hours. This process was repeated each day for the 5-day experimental period, resulting in ~240 h of video footage. The entire video footage was viewed and for each fish observed taking bites on the tile, the species and total length of each fish, number of bites, and bite location (exposed or crevice) was recorded. For those fishes that were too small to accurately identify to species, they were recorded to the lowest taxonomic level possible (typically genus). Any bites taken on the sides of the tiles were not included in counts, as propagule densities were only quantified on the upper microhabitat of the tiles. To account for differences in the availability of crevices versus adjacent exposed areas, the number of bites recorded on each microhabitat was standardised by the area of that microhabitat (i.e., crevice: 17.6 cm^2; exposed microhabitat: 103.4 cm^2).

6.2.6 Fish surveys

Herbivorous fish assemblages at each reef crest and reef flat site were quantified using three replicate 50 m belt transects. One diver recorded all larger bodied, roving herbivorous fishes from the families Acanthuridae, Kyphosidae, Labridae (tribe Scarini: parrotfishes), Pomacanthidae and Siganidae within 2.5 m of either side of the transect tape (50 x 5 m) whilst simultaneously laying the transect tape. A second diver waited two minutes, then followed the first diver and recorded the site-attached, small-bodied fishes from the families Blenniidae, Gobiidae and Pomacentridae one metre either side of the transect tape (50 x 2 m). Transects were laid parallel to the reef crest with a minimum of 10 m between adjacent transects.

6.2.7 Statistical analysis

Bayesian linear mixed models were used to analyse differences in the recruitment, growth, and mortality of *S. swartzii* propagules between crevices and exposed surfaces. Analyses were conducted in R version 3.3.2 (R Development Core Team 2016) and the models fitted in STAN with Markov chain Monte Carlo sampling (Stan Development Team 2016b, Carpenter et al. 2017) using the rstanarm package version 2.13.1 (Stan Development Team 2016a). The broom (version 0.4.4; Robinson 2017) and CODA (version 0.19.1; Plummer et al. 2006) packages were used to summarise model outputs using highest posterior density intervals with a probability level of 0.95. Plots were produced using ggplot2 version 2.2.1 (Wickham and Chang 2008).

To analyse differences in propagule density and height between crevices and flat microhabitats of tiles before deployment, two generalized linear mixed models were used. The models included microhabitat (i.e., crevice vs. exposed) as a fixed factor and microhabitat nested within tile as a random intercept, to account for the variation between quadrats within each microhabitat and tile. The density model used a gamma error distribution with a log-link transformation, whilst the height model used a Gaussian error distribution with an identity link transformation. Weakly informative priors were used on slope coefficients (density: normal(0,50), height: normal(0,10)), intercept coefficients (density: normal(0,50), height: normal(0,10)), and the error standard deviation (cauchy(0,5)), with 6000 iterations, a warmup of 3000, three chains and a thinning factor of four for both models.

To quantify changes to propagule density after exposure to herbivores, I used the proportion of propagules remaining (i.e., the post-deployment average density divided by the initial average density for the crevice and exposed areas on each tile) as the response variable. This model had the fixed factors of microhabitat (either exposed or crevice), reef zone (either reef flat or reef crest) and treatment (either caged or

uncaged). Tile identity was included as a random intercept to account for any variation in propagule densities among tiles and the non-independence of the flat and crevice microhabitats on the same tile. The model used a Gaussian error distribution with an identity link transformation. Weakly informative priors were used on slope coefficients (normal(0,5)), intercept coefficients (normal(0,10)) and error standard deviation (cauchy(0,5)), with 5000 iterations, a warmup of 2500, three chains and a thinning factor of four.

For all models, diagnostic plots were visually examined to ensure there was convergence of chains, no evidence of heteroscedasticity or autocorrelation, and that priors were sufficiently wider than the posterior values. All Rhat values were <1.05 and the ratio of effective samples to total sample size >0.6.

Planned contrasts comparing the difference in the proportion of propagules remaining between the crevice and exposed microhabitats of each tile were performed for each reef zone and treatment combination. When calculating planned contrasts, the generated model matrix was queried to estimate the probability of the difference by summing the number of slopes >0 if the estimate of the parameter was >0 (and vice versa), dividing this number by the total number of observations, and multiplying by 100 to get a percentage:

$$If\ y > 0,\ \frac{\sum a>0}{n} \times 100, else\ if\ y < 0,\ \frac{\sum a<0}{n} \times 100$$

where y = the estimated value of the slope produced by the model, a = all predicted values of the slope and n = the total number of estimated values of the slope.

6.3 Results

6.3.1 Effect of microhabitat on recruitment and growth of propagules

Prior to deploying the tiles on the reef (i.e., 18-days post-settlement), the density of propagules within crevices was 21 % higher than the density on the exposed microhabitat of the tiles (mean [95 % credible intervals]; crevices: 29.7 [26.9, 32.9] propagules cm^{-2}; exposed microhabitat: 23.4 [21.0, 25.6] propagules cm^{-2}; Fig. 6.1a). Propagules within crevices were, however, 18 % shorter than those on the exposed microhabitat (1.05 [0.95, 1.13] vs 1.27 [1.18, 1.36] mm, respectively; Fig. 6.1b).

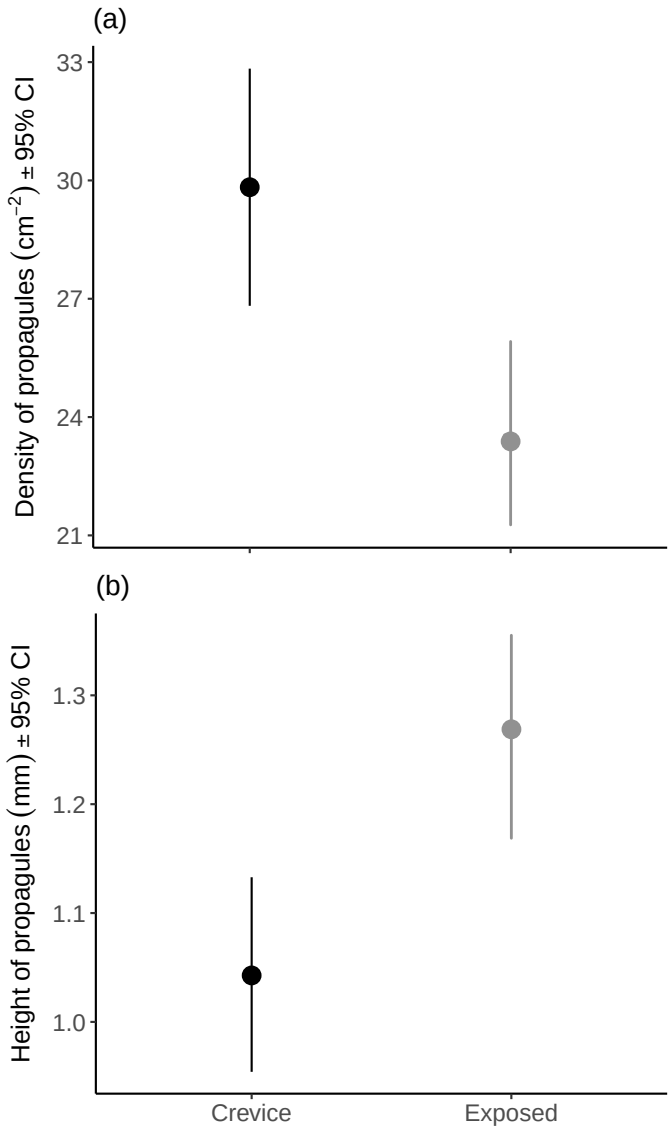

Figure 6.1: The influence of microhabitat on the recruitment and growth of *Sargassum swartzii* propagules: (a) Density of propagules in crevices and exposed surface of experimental tiles 18-days post-

settlement; (b) Average height of propagules in crevices and on flat microhabitat of tiles 18-days post-settlement. Error bars show ± 95 % Credible Intervals.

6.3.2 Effect of microhabitat on propagule survival

There were differences in the survival of propagules between microhabitats on the reef crest, but not on the reef flat (Fig. 6.2; Appendix E). Survival of propagules on the exposed surface of uncaged tiles on the reef crest was (mean [95 % credible intervals]) 0.42 [0.28, 0.56] (i.e., 42 % of the initial number of propagules remained), whereas survival in the crevices of the same tiles was 0.80 [0.66, 0.94] (Fig. 6.2; Appendix E). In contrast, survival of propagules within cages on the reef crest was similar between microhabitats: 0.68 [0.55, 0.81] on the exposed surface vs. 0.70 [0.57, 0.84] in crevices. There was less evidence of an effect of microhabitat on propagule survival for uncaged tiles on the reef flat. Survival of propagules on the exposed surface of uncaged tiles deployed on the reef flat was 0.71 [0.58, 0.85] and 0.80 [0.68, 0.95] in the crevices. For caged tiles on the reef flat, survival of propagules was 0.73 [0.57, 0.86] on the exposed surface and 0.64 [0.51, 0.79] in crevices (Fig. 6.2).

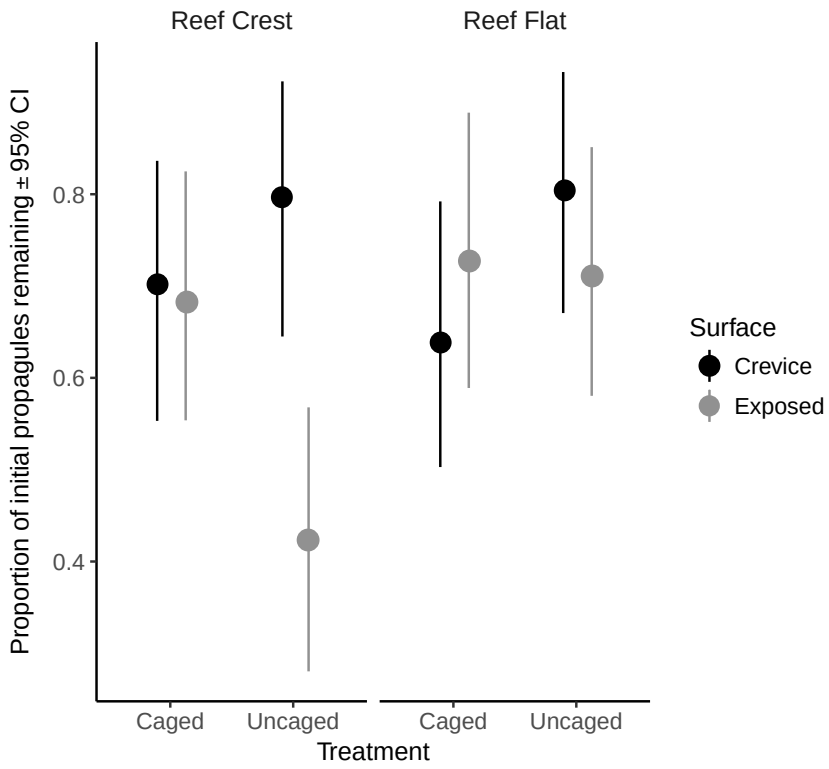

Figure 6.2: Model estimates of the survival of *Sargassum swartzii* propagules between reef zones (reef crest or reef flat), microhabitat (exposed or crevice) and treatments (caged or uncaged) after 5-day deployment ± 95 % Credible Intervals.

There was strong evidence (>99 % probability) of a difference between the proportion of propagules remaining in crevices compared to the exposed microhabitat of uncaged tiles on the reef crest, but no effect for caged tiles on the reef crest (Fig. 6.3; Appendix E). In contrast, there was only an 89.4 % probability of having more propagules remaining in the crevices than on the exposed microhabitat of the uncaged tiles on the reef flat.

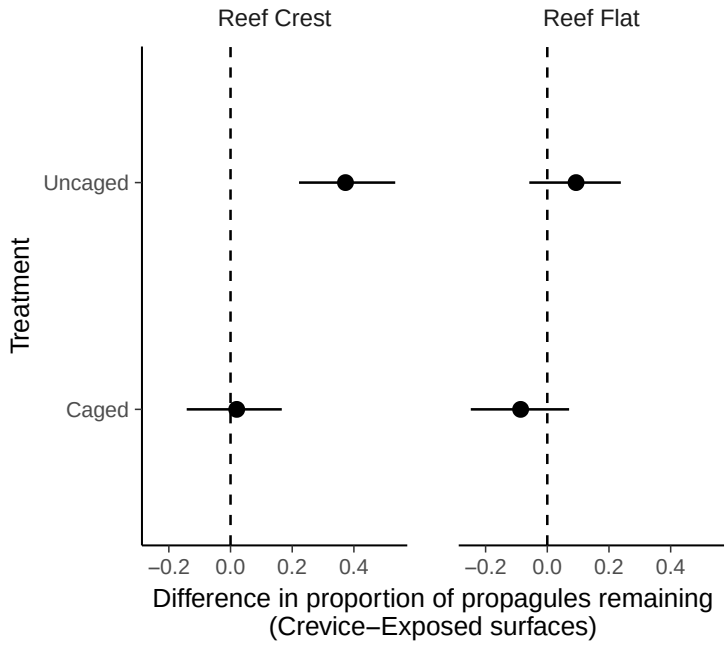

Figure 6.3: Planned contrasts comparing the survival of *Sargassum swartzii* propagules in crevices vs. exposed microhabitats of tiles, in each reef zone and treatment combination. Lines indicate 95 % credible intervals calculated using highest posterior density. Estimates (black dots) to the right of the dotted line indicate that there were, on average, more propagules in the crevices than on the exposed microhabitat of the tiles. Black dots to the left of the line would indicate that there was a higher proportion of propagules on the exposed microhabitat of the tiles than in the crevices.

Overall mean bite rates on the tiles were over 50 % greater on the reef crest (1.67 ± 0.49 bites hr^{-1} cm^{-2}) compared to the reef flat (1.02 ± 0.45 bites hr^{-1} cm^{-2}). For both reef zones the majority of bites (standardised by the area of each microhabitat) were taken from the exposed microhabitat of the tile (reef crest: 79 %; reef flat: 87 %) rather than in crevices. The majority of bites in both reef zones were taken by blennies of the genus *Ecsenius,* averaging 1.19 ± 0.20 bites hr^{-1} cm^{-2} on the exposed microhabitat and 0.27 ± 0.10 bites hr^{-1} cm^{-2} in crevices of tiles on the reef crest and 0.61 ± 0.22 bites hr^{-1} cm^{-2} on the exposed microhabitat and 0.09 ± 0.04 bites hr^{-1} cm^{-2} in the crevices of tiles on the reef flat (Fig. 6.4). The only other species that took a substantial number of bites was *Salarias fasciatus* (f. Blenniidae) which took an average of 0.21 ± 0.11 bites hr^{-1}

cm^{-2} on the exposed microhabitat and 0.03 ± 0.02 hr^{-1} cm^{-2} in crevices on the reef flat, but wasn't recorded to take any bites from tiles on the reef crest.

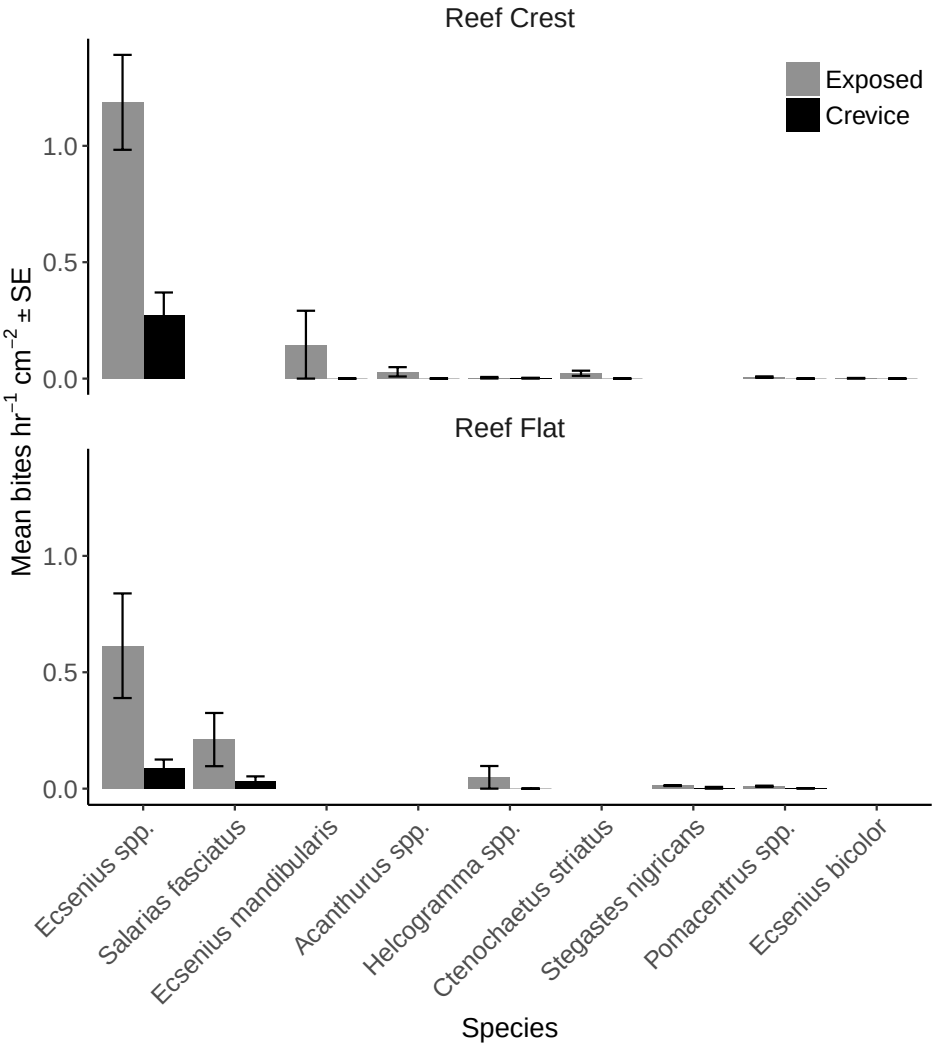

Figure 6.4: Average bite rate by fishes on exposed tiles hr^{-1} cm^{-2} (mean ± SE) between reef zones and microhabitats.

6.3.3 Fish surveys

Please see Appendix E.

6.4 Discussion

The transition between developmental stages for organisms with complex life histories often presents a bottleneck to survival (Connell 1985, Vadas et al. 1992). As such, any fitness advantage at this transition may significantly increase chances of surviving to adulthood (Keough and Downes 1982). Our results demonstrate that in areas of high herbivory, microtopographic refuges (crevices) afforded *Sargassum* propagules a survival advantage through the provision of a refuge from herbivory. Such a survival advantage may come at a cost, however, as propagules were 18 % shorter in crevices compared to those on the exposed surface of the tiles, indicating that crevices may be less favourable for early post-settlement growth. Furthermore, contrary to previous suggestions that feeding by larger-bodied grazing fishes is a major source of mortality for macroalgal propagules on coral reefs (Bellwood et al. 2004), our results suggest that small-bodied blennies, specifically of the genus *Ecsenius*, are likely to have been the primary removers of early post-settlement stage *S. swartzii*.

The refuge afforded to propagules within crevices may be particularly important for the survival of juvenile *S. swartzii*, as *Sargassum* propagules have few chemical or morphological defences (Stiger et al. 2004). On the reef crest, where herbivory is generally high (Fox and Bellwood 2007), survival of *S. swartzii* propagules on the exposed microhabitats of the tiles after 5-day exposure to local herbivore assemblages was only 42 %, compared to 80 % survival within crevices. Our findings add to the growing literature from a range of ecosystems emphasising the importance of refugia to the early post-settlement survival of organisms. Microtopographic refuges have been identified as important early post-settlement refuges for sessile organisms such as bryozoans (Keough and Downes 1982), encrusting sponges (Maldonado and Uriz 1998) and corals (Nozawa 2008). Indeed, Franco et al. (2015) reported that rates of herbivory on temperate reefs in Portugal structured the distribution of *Laminaria* (kelp)

recruits; in areas where herbivory was high, most recruits occurred in crevices, whereas in areas where herbivory was low, the majority of recruits were found in exposed locations. This is consistent with our findings that crevices were important for the survival of *Sargassum* propagules in areas where herbivory was high (i.e., the reef crest) but were not as important to survival in areas with lower levels of herbivory (i.e., the reef flat), at least over the 5-day temporal scale of this study.

Although settling within crevices appears to confer a survival advantage for *S. swartzii* propagules, it may come at a cost. Eighteen days after settlement, the height of *Sargassum* propagules within crevices was 18 % lower than propagules that had settled to the exposed microhabitats of the tiles. This lower growth within crevices could be related to different light and water flow regimes within crevices compared to exposed microhabitats, and/or density-dependent factors. Unlike other algal species (Christie 1973), *Sargassum* propagules are non-motile, and it is therefore likely that the higher initial density in crevices was a result of the negatively buoyant propagules being 'trapped' in a crevice and settling rather than actively choosing to settle in this microhabitat (Norton and Fetter 1981). Kendrick (1994) reported that the growth of temperate *Sargassum* recruits was negatively related to density, indicating that there may be a trade-off between survival and growth within crevices and on exposed surfaces (Amsler et al. 1992, Bergey 1999, Bergey 2005, Brandl et al. 2014). Our results suggest that the benefits of settling in a crevice may only outweigh the disadvantages when rates of herbivory are high, by enhancing propagules' survival at a stage characterised by high mortality (Kendrick and Walker 1995, Brandl et al. 2014, Franco et al. 2015). However, the slower growth of propagules within crevices may mean that they are subject to consumption by grazing organisms for longer (i.e., the

stage-duration hypothesis (Leggett and Deblois 1994)) which could partially or completely negate any protective value of the crevices.

Rapid increases in algal biomass following the exclusion of large herbivores has led to the widely-held assumption that large-bodied grazing fishes, such as surgeonfishes and parrotfishes, are primarily responsible for the removal of macroalgal propagules in the EAM (Diaz-Pulido and McCook 2003, Bellwood et al. 2004). Our results question this assumption and suggest that small-bodied blennies (*Ecsenius* spp.) may also play an important role in the early post-settlement mortality of macroalgal propagules, as these fishes took a disproportionately higher number of bites on uncaged tiles than any other grazing fishes. Grazing by the combtooth blenny *Salarias fasciatus* has been demonstrated to reduce the survival of early-post settlement coral recruits (Christiansen et al. 2009), even though *S. fasciatus* are thought to primarily consume detrital aggregates within the EAM (Wilson 2000). *Ecsenius* spp. may similarly reduce propagule survival through grazing of the EAM even though detrital aggregates may be the primary target (Wilson 2000). Although our results suggest that blennies contribute to the mortality of small (<2 mm) *Sargassum* propagules (up to 25-days post-settlement), it is likely that *Sargassum* and other macroalgal propagules will quickly reach a size refuge from blennies as they grow (Lubchenco 1983, Briggs et al. 2018). It is yet to be determined if propagule removal by blennies at this early post-settlement stage could translate to lower final densities of adult macroalgae, or if other species of grazing fishes consume larger macroalgal propagules.

Our findings also suggest that the importance of microtopographic refuges for the survival of macroalgal propagules varies among reef zones. On the reef flat, where conditions for *Sargassum* growth are favourable (McCook 1996) and herbivory is generally low (Hay 1981, Fox and Bellwood 2007), the survival of *Sargassum*

propagules did not differ between caged and uncaged tiles. This result is consistent with the findings of previous studies showing that the density and/or biomass of herbivorous fishes (Lewis and Wainwright 1985, Wismer et al. 2009) and rates of herbivory (Hay 1981, Fox and Bellwood 2007), are lower on the reef flat than the reef crest, and have led to suggestions that the reef flat is a spatial refuge from herbivory (Hay et al. 1983, Lewis and Wainwright 1985). In areas of lower herbivory, refuges may be less critical for the survival of *Sargassum* propagules (Franco et al. 2015).

The results of our study highlight the potential importance of crevices for the early post-settlement survival and growth of *S. swartzii,* however, further research is needed to investigate how the size of refugia and the potential agents of mortality (i.e., herbivores) change with macroalgae size and vary among macroalgal taxa. Whilst crevices were of uniform size in the present study, the size and depth of crevices relative to propagule size is likely to have a large influence on the degree of protection afforded to propagules (Lubchenco 1983, Bergey 1999). Furthermore, the fish species responsible for the removal of propagules are likely to change as the juvenile *Sargassum* grows. It is unknown which fishes remove these larger (0.5-5 cm) juveniles, if the phenolic content of *S. swartzii* increases ontogenetically, as in *Sargassum mangarevense* (Stiger et al. 2004), possibly decreasing susceptibility to herbivores with age, nor if the protective value of the crevices for early post-settlement propagules significantly affects rates of survival to maturity.

The results of the present study provide a useful insight into the value of microtopographic refuges for the recruitment, growth and survival of newly-settled *Sargassum* propagules, and is one of the first to highlight the potential role of blennies in consuming newly-settled macroalgal propagules on coral reefs. Microtopographic refuges on coral reefs can provide newly-settled propagules a refuge from grazing in

this vulnerable early post-settlement stage. Higher early-post settlement survival of propagules within refuges may facilitate the spread and persistence of *Sargassum* communities on coral reefs, particularly in areas where herbivory pressure is high.

Chapter 7: General discussion

Coral reefs are among the most threatened ecosystems on the planet, subject to sustained and ongoing degradation throughout the world (Jackson et al. 2001, De'ath et al. 2012, Hughes et al. 2017b). Degradation of coral reefs is manifest as extensive loss of habitat-forming and reef-building corals, which are increasingly being replaced by macroalgae as the dominant structural element and cover in shallow reef environments (Hughes 1994, Rasher et al. 2013, Graham et al. 2015). Investigating the mechanisms underpinning and reinforcing coral to macroalgae regime shifts is central to predicting, managing and reversing widespread coral reef degradation. While there are a number of factors that contribute to these shifts, control of primary production by herbivores is believed to be a central process mediating shifts between coral and macroalgae (Hughes et al. 2007, Rasher et al. 2013, Graham et al. 2015). Subsequently, a large body of research has quantified how rates of removal of macroalgae (i.e., potential reversal of a regime shift) vary spatially (Hay 1981, Fox and Bellwood 2007, Bennett and Bellwood 2011, Chong-Seng et al. 2014), temporally (Hay et al. 1983, Lefèvre and Bellwood 2011), among macroalgal taxa (Mantyka and Bellwood 2007b, Rasher et al. 2013), and among macroalgae with differing nutritional compositions (Diaz-Pulido and McCook 2003). These studies have, however, focussed on the consumption of the leafy, adult macroalgal thalli, and have not considered the susceptibility of different life-history stages (e.g., propagules) or components of macroalgae (e.g., holdfasts) to herbivores, or the susceptibility of macroalgae to disturbance.

Research presented in this thesis represents the most holistic and comprehensive study thus far conducted into the ecology and herbivory of *Sargassum*. Through examining the susceptibility and resilience of *Sargassum* to herbivory and disturbance, this thesis highlights the critical importance of considering the ecology of *Sargassum*,

or indeed any other macroalgae, when investigating how herbivory can shape populations and assemblages of macroalgae. Chapter 2 explicitly compared the resilience of *Sargassum* and coral communities to multiple disturbances in the northern Great Barrier Reef, showing that recovery of *Sargassum* communities can occur within one to two years post-disturbance, in contrast to corals which showed no evidence of recovery in the same time frame. I then used an experimental approach (Chapter 3) to simulate the effects of a storm on *Sargassum*-dominated assemblages, finding that the recovery of *Sargassum* biomass was rapid and largely attributable to regrowth from holdfasts remaining on the substratum. Given the importance of regrowth from *Sargassum* holdfasts, Chapter 4 investigated the resistance and resilience of *Sargassum* holdfasts to herbivory, showing that herbivorous fishes were extremely reluctant to feed on holdfasts and rarely inflicted any damage to holdfasts, even during incidental grazing on adjacent substrates. Moreover, when holdfasts were damaged experimentally, *Sargassum* had an exceptional capacity to regrow from damaged holdfasts; there was no detectable effect of removing half the holdfast on the subsequent growth or survivorship of *Sargassum* after one year. Chapters 5 and 6 investigated, for the first time, herbivory of early post-settlement *Sargassum* propagules, finding that blennies, rather than larger-bodied grazers, may significantly contribute to the removal of early post-settlement propagules. Chapter 5 showed that the presence of *Sargassum* propagules within the EAM can lower rates of grazing, suggesting that grazing fishes may avoid feeding on areas containing propagules. Chapter 6 provided evidence that the survival of *Sargassum* propagules on coral reefs may be enhanced by settling within crevices, gaining refuge from herbivory. In considering the ecology of a focal species, I present new evidence as to why

macroalgae-dominated regimes can be so difficult to reverse once established, namely, high capacity to recover following disturbance and resistance to herbivory.

This thesis identified that the rapid recovery of *Sargassum* after disturbance is primarily due to regrowth from holdfasts, though this may be supplemented by the recruitment and growth of propagules. While numerous studies have documented the rapid consumption of macroalgal biomass (Hoey and Bellwood 2009, Vergés et al. 2011, Rasher et al. 2013), this consumption may have little impact on macroalgal populations unless the holdfast is removed. However, herbivores seem to avoid biting and, consequently, removing holdfasts. Coupled with the capacity of *Sargassum* (and potentially other macroalgae) to rapidly regrow from even severely damaged holdfasts (Chapters 3 and 4), this highlights its potential resilience to herbivory and disturbance, and the critical importance of considering the ecology of both the consumer and its resource when assessing outcomes of biological interactions.

The persistence of *Sargassum* on reefs likely arises from both its capacity to regrow from holdfasts (Chapter 3), including those that have sustained damage (Chapter 4), and high reproductive output facilitating growth from propagules (Engelen et al. 2005). Both components are likely to be important; regrowth from holdfasts allows fast recovery from storm disturbances (Chapter 3), and the spread of propagules allows colonisation of new areas and fast recovery of the canopy if adults have been entirely removed (Kendrick and Walker 1994). In contrast to the typical decadal recovery of corals (Graham et al. 2011, Linares et al. 2011, Gilmour et al. 2013), the opportunistic nature of *Sargassum* allows it to rapidly expand and colonise new areas. Further contributing to the persistence and expansion of *Sargassum* is the reluctance of herbivores to consume holdfasts (Chapter 4), lower grazing rates on EAM containing

Sargassum propagules (Chapter 5) and refuge from herbivory within crevices for propagules settling on the reef (Chapter 6).

In terrestrial ecosystems, areas of intense grazing by mammalian herbivores are often characterised by a low standing biomass of productive grasses, a 'grazing lawn' (McNaughton 1984, Hempson et al. 2015). The non-selective, or incidental, consumption of seedlings of larger woody shrubs and trees within the lawn prevents their establishment and maintains the lawn in a productive state (McNaughton 1984, Olff et al. 1999). This concept of grazing lawns has often been applied to both temperate and tropical marine ecosystems, but rarely tested. In this thesis, I investigated if grazing fishes removed macroalgae (*Sargassum*) propagules within the EAM (*sensu* 'grazing lawn') and if the presence of macroalgae propagules influenced the feeding preferences of grazing fishes. Contrary to expectations, I found evidence that some grazers were able to detect propagules within the EAM, decreasing their feeding rates in these areas, and therefore did not display non-selective grazing of the EAM as has been previously assumed (Bellwood et al. 2004). Indeed, the lower grazing rates on EAM containing *Sargassum* propagules may contribute to the establishment and persistence of *Sargassum* populations on coral reefs (Chapter 2), however, this needs to be examined with further research.

This thesis also considered the likelihood of storms clearing reefs of macroalgal biomass, essentially resetting the system and potentially providing a 'window of opportunity' for the recovery of coral populations (Graham et al. 2013). Results from Chapters 2 and 3 indicate that any window of opportunity is more likely to favour the recovery and expansion of *Sargassum* rather than the recovery of corals, as recovery of coral-dominated systems can take 5-10 years (Graham et al. 2011, Linares et al. 2011, Gilmour et al. 2013), in contrast to the 1-2 years for macroalgae-dominated reefs

(Chapter 2). *Sargassum* not only rapidly recovered post-disturbance, but also extended its range into areas where it was previously absent. Proliferation of *Sargassum* into previously coral-dominated areas may inhibit future coral recovery (Hughes et al. 2007), and is unlikely to provide an opportunity for the recovery of corals, unless there is a simultaneous and rapid increase in herbivory.

The findings of this thesis suggest that pulse disturbances are unlikely to cause long-term decreases in *Sargassum* abundance, due to the rapid regrowth that was likely fuelled by energy reserves in the holdfast (Wong 2007). Sustained browsing of emergent regrowth may deplete the holdfast's energetic reserves and ultimately lead to the mortality of the alga. Indeed, high levels of mannitol within the holdfast in *Sargassum siliquastrum* have been suggested to support holdfast maintenance during senescence and regrowth of fronds in the next growing season (Prince and Daly Jr 1981, Wong 2007). The holdfasts of *Sargassum horneri* have a net photosynthetic rate close to zero, suggesting that holdfasts have little capacity for photosynthesis and thus have finite energy reserves (Gao 1991). As a consequence, energy reserves within the holdfast are likely to be depleted by constant regrowth, until ultimately the holdfast becomes incapable of producing fronds (Gomez and Westermeier 1991). However, it is unknown what level of sustained browsing is required to exhaust reserves within the holdfast.

The results of this thesis have direct implications for the growing emphasis to rehabilitate macroalgae-dominated reefs through the manual removal of macroalgal biomass (Ceccarelli et al. 2018). These 'weeding' programs are unlikely to succeed without large concomitant changes to the drivers of the original decline (i.e. chronic disturbances). The high resilience of *Sargassum* to disturbances that leave the holdfast intact means that holdfasts would have to be completely removed to have any

substantive effect on *Sargassum* biomass during the next growing season (Chapter 3). However, such programs often rely on volunteers and may only partially remove the holdfast, with regeneration of *Sargassum* from any remaining holdfast fragments likely (Chapter 4). Even when holdfasts are completely removed, new recruits could recover up to 50 % of the 'natural' biomass within one year (Chapter 3). The success of macroalgal programs for reef restoration appear reliant on the use of humans as 'herbivores' to continually remove algal biomass, and as such, are likely only feasible for small, easily managed areas. There is an urgent need for conservation efforts to shift away from small scale restoration programs to focus on addressing the larger drivers of decline if we are to conserve reefs into the future.

The findings of this thesis have given rise to several areas of potential future research. Specifically, results from Chapter 4 suggest that herbivores seemingly avoid *Sargassum* holdfasts when feeding. Direct removal of holdfasts may not be necessary if perpetual browsing of *Sargassum* can cause mortality of the holdfast, however, the rate of herbivory required to cause mortality of a *Sargassum* individual is currently unknown. Further, the lower grazing rates on areas of EAM containing *Sargassum* propagules indicates that there may be a previously unrecognised positive feedback within *Sargassum*-dominated areas, and further research could investigate if the EAM containing propagules adjacent to *Sargassum* beds experiences lower grazing rates than areas further away from adult *Sargassum*, potentially enhancing propagule survival close to adults (Dell et al. 2016). It is also unknown how removal of early-post settlement propagules by blennies affects rates of propagule survival to adulthood (Chapters 5 and 6), and, indeed, which fishes remove juvenile *Sargassum* after it has reached a size refuge from blennies.

This thesis examined the ecology of two species of *Sargassum* on the GBR, however, shifts to other genera of macroalgae such as *Lobophora* spp. have also been reported on reefs worldwide (Cheal et al. 2010, Roff et al. 2015). Whilst the findings of this thesis may translate well to other species of tropical *Sargassum* that have similar cycles of senescence and regrowth, reefs dominated by other macroalgae in other locations are likely subject to their own unique processes; further research is needed to examine the mechanisms underpinning shifts in these locations.

Into the future, it is predicted that the intensity and frequency of disturbances affecting coral reefs will increase (Knutson et al. 2010, Hughes et al. 2018). The results from this thesis suggest that *Sargassum* is more resilient to disturbance than corals, however, it remains to be seen how future predicted increases in disturbance frequency and intensity will affect both *Sargassum* and coral cover. *Sargassum* may become more common on reefs in the future than it is today. Consequently, it is imperative to understand the processes operating within *Sargassum*, and other macroalgae, beds that enhance their persistence and proliferation, and ways in which they may be controlled. The results of this thesis have provided new insights into the dynamics of *Sargassum* communities, increasing our understanding of the mechanisms underpinning the stability of *Sargassum*-dominated assemblages and the difficulties of reverting back to coral-dominance.

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Appendix A: Supplemental information for Chapter 2

Table A1: Model output of Sargassaceae count data from transects at five sites between 2013-2017.

term	estimate	std.error	conf.low	conf.high
(Intercept)	-0.503	0.614	-1.700	0.608
Year2014	-4.321	2.075	-8.375	-0.429
Year2015	-0.561	0.966	-2.472	1.236
Year2016	0.988	0.761	-0.427	2.548
Year2017	1.395	0.721	0.096	2.943
Site3	4.841	0.665	3.501	6.082
Site5	4.476	0.663	3.197	5.752
Site2	-2.355	1.546	-5.352	0.482
Site4	4.824	0.652	3.585	6.032
Year2014:Site3	-5.115	3.115	-11.479	0.521
Year2015:Site3	-1.174	1.013	-3.144	0.810
Year2016:Site3	-1.182	0.839	-2.752	0.487
Year2017:Site3	-1.674	0.810	-3.342	-0.223
Year2014:Site5	2.914	2.087	-0.951	6.940
Year2015:Site5	-4.231	1.217	-6.586	-1.698
Year2016:Site5	-1.870	0.851	-3.661	-0.278
Year2017:Site5	-1.601	0.813	-3.289	-0.143
Year2014:Site2	-1.524	4.127	-9.949	5.921
Year2015:Site2	2.404	1.845	-1.295	6.060
Year2016:Site2	3.664	1.628	0.468	6.689
Year2017:Site2	4.812	1.580	1.977	7.996
Year2014:Site4	2.441	2.089	-1.407	6.591
Year2015:Site4	-2.043	1.048	-3.990	-0.039
Year2016:Site4	-1.865	0.835	-3.482	-0.178
Year2017:Site4	-1.642	0.803	-3.151	-0.090
reciprocal_dispersion	4.368	1.608	1.897	7.527
mean_PPD	23.513	2.856	18.270	29.290
log-posterior	-313.724	4.374	-322.132	-305.251

Table A2: Model output of coral count data from transects at five sites between 2013-2017

term	estimate	std.error	conf.low	conf.high
term	3.393	0.347	2.765	4.095
(Intercept)	-3.592	0.742	-4.969	-2.081

Year2014	-2.475	0.582	-3.571	-1.266
Year2015	-2.139	0.563	-3.279	-1.060
Year2016	-1.848	0.562	-2.917	-0.717
Year2017	-0.812	0.502	-1.840	0.137
Site3	-1.365	0.530	-2.361	-0.257
Site5	0.475	0.510	-0.549	1.430
Site2	-2.482	0.597	-3.642	-1.316
Site4	-4.508	3.166	-10.870	0.614
Year2014:Site3	-0.144	0.951	-2.007	1.570
Year2015:Site3	-2.224	1.388	-4.855	0.417
Year2016:Site3	-1.577	1.059	-3.445	0.631
Year2017:Site3	2.973	0.962	1.008	4.781
Year2014:Site5	-4.774	2.945	-11.041	-0.052
Year2015:Site5	-4.892	2.928	-10.883	-0.194
Year2016:Site5	-0.248	0.932	-1.975	1.697
Year2017:Site5	3.644	0.935	1.864	5.526
Year2014:Site2	-0.261	0.814	-1.845	1.347
Year2015:Site2	-0.875	0.847	-2.671	0.660
Year2016:Site2	-0.100	0.786	-1.589	1.431
Year2017:Site2	3.027	1.035	1.114	5.110
Year2014:Site4	0.691	1.124	-1.600	2.781
Year2015:Site4	1.905	0.919	0.246	3.871
Year2016:Site4	0.032	1.153	-2.327	2.106
Year2017:Site4	2.217	0.962	0.825	4.237
reciprocal_dispersion	8.126	2.183	4.760	12.420
mean_PPD	-238.709	4.582	-248.322	-230.817

Appendix B: Supplemental information for Chapter 3

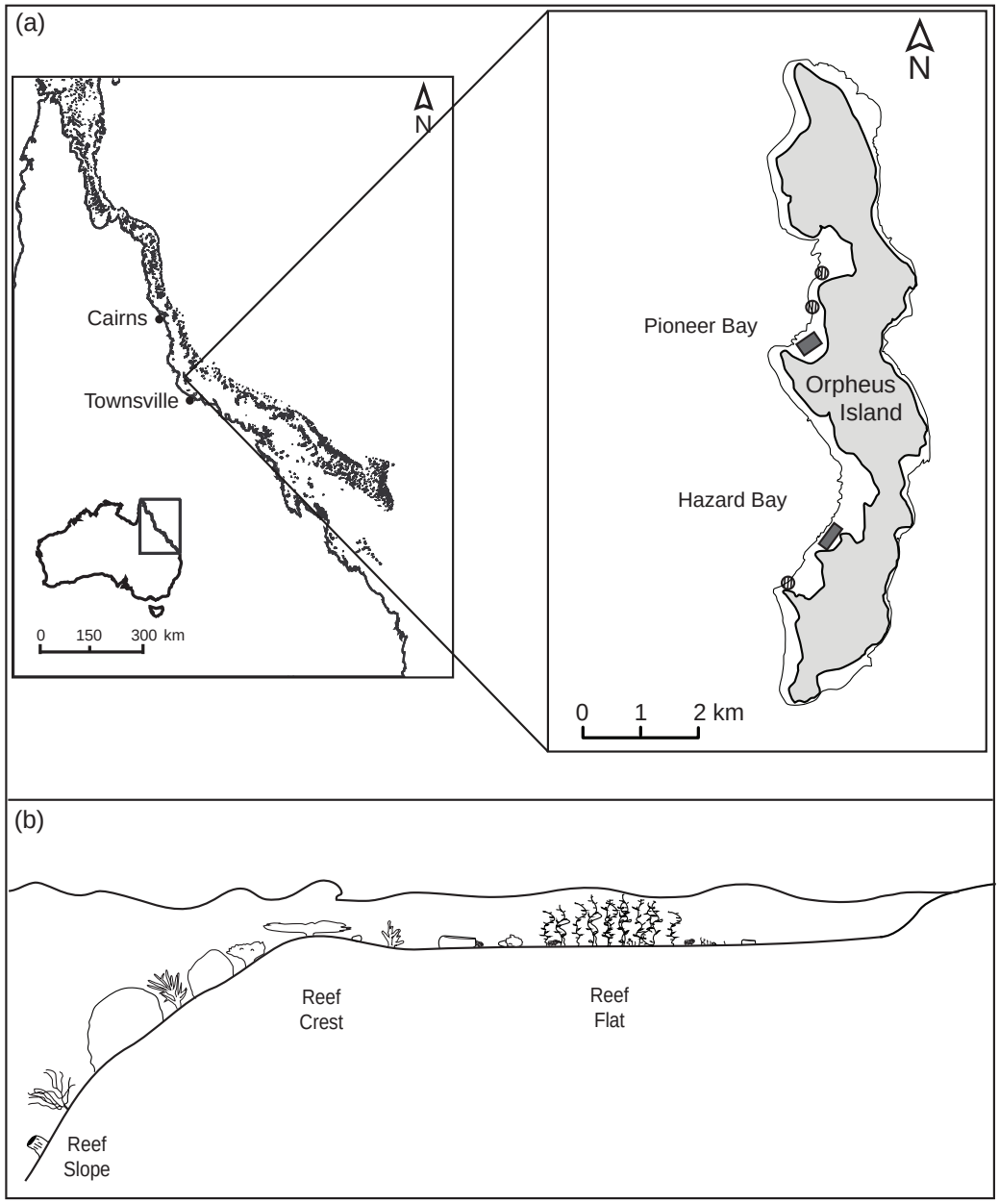

Figure B1: (a) Map of field site locations at Orpheus Island for the regrowth of *Sargassum* after disturbance experiment (grey rectangles) and the locations of transplanted rocks for herbivore mediated holdfast removal (lined circles); (b) schematic of reef flat, crest and slope characteristics, with *Sargassum* abundance high on the mid reef flat.

Table B1: Details of the locations and treatments of rocks that could not be relocated at the conclusion of the study

Bay	Treatment	Number of rocks not relocated

Little Pioneer Bay	Uncaged	3
	Initially uncaged	0
	Caged	0
Pioneer Bay	Uncaged	2
	Initially uncaged	2
	Caged	2
Hazard Bay	Uncaged	2
	Initially uncaged	1
	Caged	0

Table B2: AICc values for candidate models of *Sargassum* height and density in order to determine the best model for describing the data. The AICc in bold is the lowest value of the compared models and indicates the model of best fit.

Data	Model	AICc	df	Goodness of fit
Height (log transformed)	Interactive	-84.29	14	
	Interactive + autoregressive correlation structure	-105.64	15	
	Additive	-99.14	8	
	Additive + autoregressive correlation structure	**-120.44**	9	$R^2_{marginal}$ = 0.82, $R^2_{conditional}$ = 0.83
Density (sqrt transformed)	Interactive	270.68	14	
	Interactive + autoregressive correlation structure	272.78	15	
	Additive	**261.98**	8	$R^2_{marginal}$ = 0.23, $R^2_{conditional}$ = 0.84
	Additive + autoregressive correlation structure	263.73	9	

Table B3: Additive model summary of holdfast density data with fixed effects Time and Treatment.

Factors	Value	Std. Error	DF	t-value	p-value
(Intercept)	6.02	0.56	83	10.8	<0.001
Time - Month 7	1.18	0.22	83	5.4	<0.001
Time - Month 9	1.30	0.22	83	6.0	<0.001

Time - Month 11	1.38	0.22	83	6.3	<0.001
Treatment - Control	1.39	0.19	83	7.3	<0.001
Treatment - Trimmed	1.62	0.19	83	8.5	<0.001

Table B4: Tukey's HSD pairwise comparisons of treatments from holdfast density data

Groups	Estimate	Std. Error	Z value	Pr (> |z|)
Removed, Control	1.39	0.19	7.33	<0.001
Removed, Trimmed	1.62	0.19	8.53	<0.001
Control, Trimmed	0.23	0.19	1.20	0.453

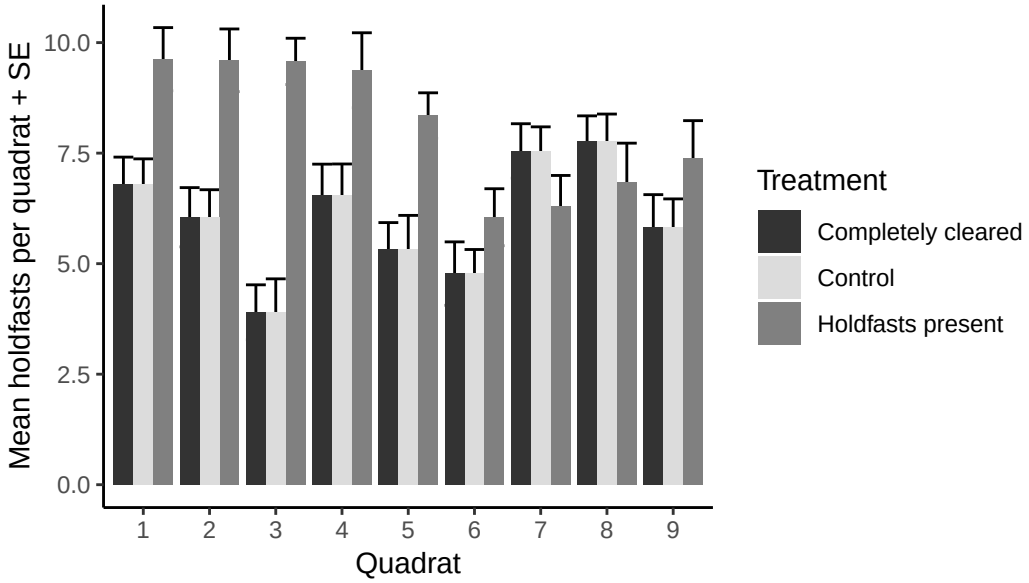

Figure B2: Average number of holdfasts within quadrats 1-9 + SE, with quadrat 5 occurring within the centre of the plot area.

Table B5. Additive model summary of height data with fixed effects Time and Treatment.

Factors	Value	Std. Error	DF	t-value	p-value
(Intercept)	0.59	0.04	83	13.2	<0.001
Time - Month 7	0.25	0.04	83	5.84	<0.001
Time - Month 9	0.64	0.05	83	12.5	<0.001
Time - Month 11	0.72	0.06	83	13.0	<0.001

Treatment - Control	0.22	0.02	83	10.0	<0.001
Treatment - Trimmed	0.23	0.02	83	9.42	<0.001

Table B6: Tukey's HSD pairwise comparisons of treatments from height data

Groups	Estimate	Std. Error	Z value	Pr (> |z|)
Removed, Control	0.22	0.02	10.0	<0.001
Removed, Trimmed	0.22	0.02	9.42	<0.001
Control, Trimmed	0.01	0.02	0.22	0.974

Table B7. Analysis of deviance table (Type II Wald Chi-square test) of number of holdfasts on rocks between months (i.e. before and after experiment) and treatment.

Factors	χ^2	Df	Pr (>Chisq)
Month	14.72	1	<0.001
Treatment	6.39	2	<0.05
Month x Treatment	12.15	2	<0.01

Table B8. Before and after average diameters of holdfasts in each treatment.

Treatment	Average diameter before (mm)	Average diameter after (mm)	Change in diameter (mm)
Caged	8.98	10.29	+ 1.31
Initially exposed	8.45	10.57	+ 2.11
Exposed	7.60	8.45	+ 0.86

Appendix C: Supplemental information for Chapter 4

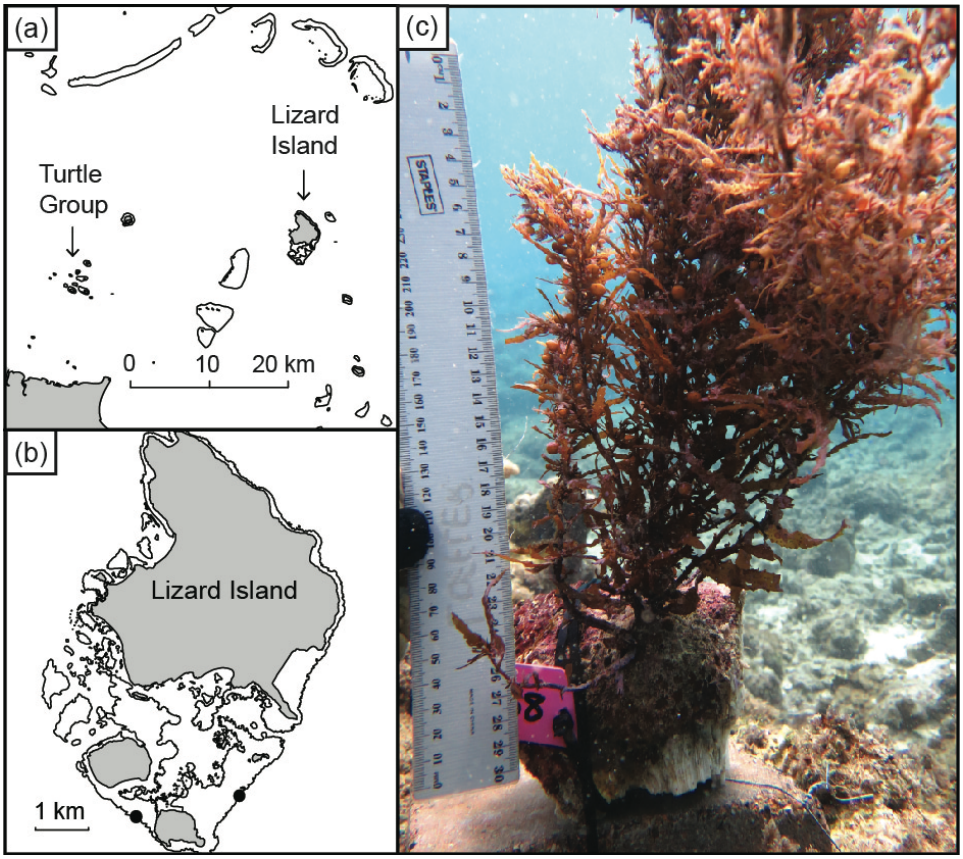

Figure C1: (a) Relative position of the Turtle Group and Lizard Island. The landmass in the bottom left corner is the Australian mainland; (b) Location of study sites on Lizard Island where assays were deployed (black circles); (c) Example of assay setup on the reef crest showing *S. swartzii* thallus and holdfast growing on a piece of reef pavement. This was attached to a paving tile with a cable tie. The paving tile was secured to the reef using thin wire threaded through natural holes in the reef and through a central hole in the paver.

Table C1: List of each fish species and the sum of bites taken on *S. swartzii* and rocks, ordered by sum of bites on *S. swartzii.*

Species	Sum of bites on *S. swartzii*	Sum of bites on rock
Naso unicornis	4806	183
Siganus doliatus	1332	376
Siganus corallinus	574	173
Ctenochaetus striatus	451	957
Acanthurus nigrofuscus	383	1803

Siganus canaliculatus	207	21
Zebrasoma veliferum	149	172
Acanthurus dussumieri	124	64
Acanthurus nigricauda	78	87
Acanthurus blochii	32	15
Naso annulatus	16	0
Pomacanthus semicirculatus	13	54
Scarus niger	12	191
Chlorurus microrhinos	11	12
Siganus punctatus	4	0
Sufflamen chrysopterum	3	17
Naso doliatus	2	0
Pomacentrus wardi	1	0
Chlorurus spilurus	0	140
Zanclus cornutus	0	110
Scarus frenatus	0	39
Chlorurus bleekeri	0	35
Pomacanthus sexstriatus	0	29
Scarus rivulatus	0	19
Scarus oviceps	0	15
Scarus schlegeli	0	12
Scarus globiceps	0	11
Scarus dimidiatus	0	4
Balistapus undulatus	0	2
Scarus psittacus	0	2
Thalassoma jansenii	0	2
Scarus ghobban	0	1

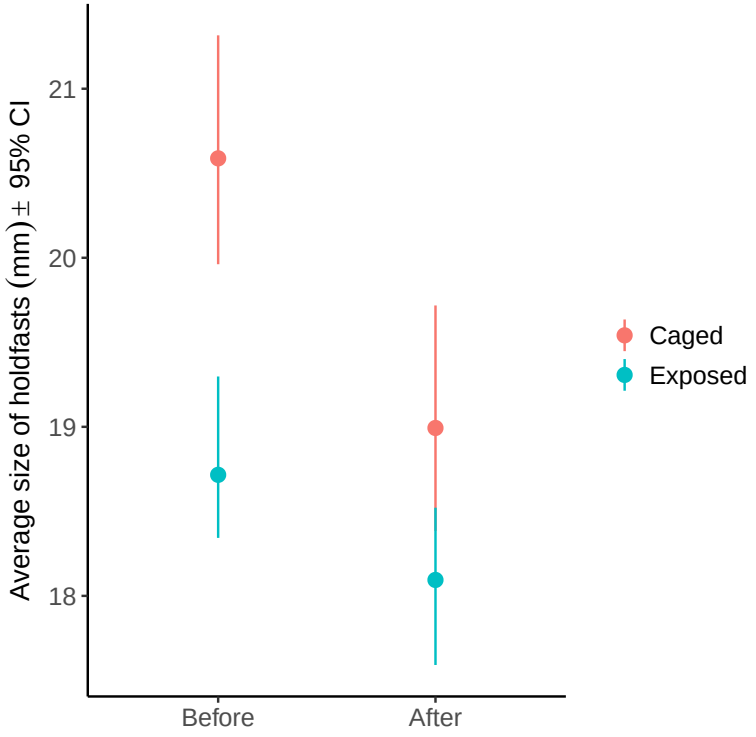

Figure C2: Average size (mm) of exposed and caged *S. swartzii* holdfasts before and after 24-day deployment on the reef crest.

Table C2: Modelled values of holdfast diameter before and after deployment between caged and exposed rocks

term	estimate	std.error	conf.low	conf.high	rhat	ess
(Intercept)	20.588	1.025	18.628	22.619	0.998	1469
DateAfter	-1.595	1.464	-4.310	1.346	0.998	1500
treat.ctrlExposed	-1.872	1.238	-4.212	0.441	0.998	1481
DateAfter:treat.ctrlExposed	0.973	1.749	-2.640	4.200	0.999	1374
sigma	4.937	0.296	4.360	5.478	0.999	1490
mean_PPD	18.824	0.585	17.657	19.965	1.000	1500
log-posterior	-461.255	1.618	-464.428	-458.873	0.998	1500

Table C3: Modelled values of nitrogen content among *S. swartzii* components

term	estimate	std.error	conf.low	conf.high	rhat	ess
(Intercept)	0.798	0.053	0.697	0.901	1.000	1500
PartStipe	-0.319	0.073	-0.461	-0.185	1.000	1500
PartBlade	0.004	0.061	-0.110	0.126	1.001	1500

b[(Intercept) Rep:1]	0.003	0.031	-0.060	0.070	0.999	1500
b[(Intercept) Rep:2]	-0.001	0.030	-0.069	0.064	0.999	1500
b[(Intercept) Rep:3]	0.000	0.030	-0.061	0.072	1.000	1500
b[(Intercept) Rep:4]	-0.008	0.031	-0.076	0.058	1.000	1492
b[(Intercept) Rep:5]	0.011	0.032	-0.048	0.086	1.004	1438
b[(Intercept) Rep:_NEW_Rep]	0.000	0.042	-0.085	0.095	1.001	1500
sigma	0.112	0.021	0.075	0.152	0.999	1500
Sigma[Rep:(Intercept), (Intercept)]	0.002	0.004	0.000	0.008	0.998	1500
mean_PPD	0.720	0.035	0.659	0.796	1.001	1439
log-posterior	-2.461	2.530	-7.403	2.019	0.999	1500

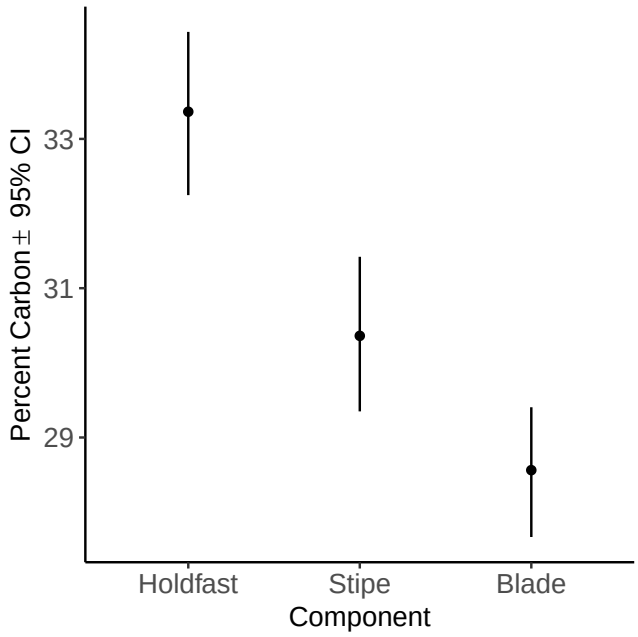

Figure C3: Percent carbon in *S. swartzii* components, presented as mean ± 95% credible intervals.

Table C4: Modelled values of carbon content among *S. swartzii* components

term	estimate	std.error	conf.low	conf.high	rhat	ess
(Intercept)	33.365	0.553	32.247	34.434	1.000	1500
PartStipe	-3.003	0.707	-4.296	-1.624	1.000	1500
PartBlade	-4.802	0.631	-6.072	-3.578	1.000	1467
b[(Intercept) Rep:1]	0.084	0.368	-0.687	0.885	0.999	1500
b[(Intercept) Rep:2]	0.003	0.375	-0.781	0.776	0.999	1500
b[(Intercept) Rep:3]	-0.163	0.381	-1.008	0.506	0.999	1490

b[(Intercept) Rep:4]	-0.135	0.389	-0.999	0.598	0.999	1383
b[(Intercept) Rep:5]	0.273	0.420	-0.332	1.232	0.999	1500
b[(Intercept) Rep:_NEW_Rep]	0.007	0.502	-0.973	1.244	0.999	1311
sigma	1.120	0.221	0.731	1.561	0.998	1426
Sigma[Rep:(Intercept), (Intercept)]	0.278	0.500	0.000	1.126	1.001	1407
mean_PPD	30.227	0.359	29.496	30.912	1.002	1424
log-posterior	-50.927	2.712	-56.382	-45.993	0.999	1377

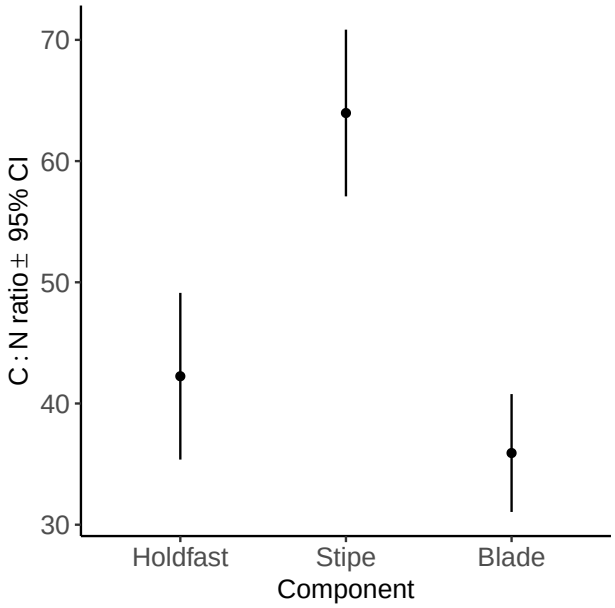

Figure C4: Ratio of carbon to nitrogen in *S. swartzii* components, presented as mean ± 95% credible intervals. The stipe component had a significantly higher C:N ratio than the holdfast and blade components.

Table C5: Modelled values of carbon to nitrogen ratio among *S. swartzii* components

term	estimate	std.error	conf.low	conf.high	rhat	ess
(Intercept)	43.379	4.410	34.468	51.406	1.002	1500
PartStipe	21.348	6.005	8.836	32.731	1.000	1500
PartBlade	-7.145	5.072	-16.786	2.804	0.999	1500
b[(Intercept) Rep:1]	-0.203	2.571	-5.206	4.615	1.002	1326
b[(Intercept) Rep:2]	-0.315	2.433	-5.850	4.389	1.004	1143
b[(Intercept) Rep:3]	-0.450	2.382	-6.269	3.683	1.001	1232
b[(Intercept) Rep:4]	0.180	2.565	-4.870	5.253	1.001	1219
b[(Intercept) Rep:5]	0.433	2.473	-3.675	6.109	1.000	1500

b[(Intercept) Rep:_NEW_Rep]	0.115	3.488	-6.392	6.763	1.000	1500
sigma	9.204	1.750	6.301	12.787	1.002	1489
Sigma[Rep:(Intercept), (Intercept)]	11.436	39.086	0.000	48.539	1.001	1077
mean_PPD	45.007	2.930	39.681	51.521	1.003	1500
log-posterior	-95.085	2.590	-99.907	-90.234	1.002	1314

Table C6: Modelled values of holdfast mortality

term	estimate	std.error	conf.low	conf.high	rhat	ess
(Intercept)	61.164	10.174	41.723	81.228	1.001	1231
DamageHalf	-34.630	10.662	-54.210	-12.045	1.000	1443
DamageQuarter	-54.030	10.930	-78.387	-34.287	1.000	1367
DamageControl	-40.338	10.954	-61.222	-18.262	1.001	1318
b[(Intercept) Patch:1]	-2.949	9.026	-23.404	13.376	0.999	1397
b[(Intercept) Patch:2]	-3.132	9.330	-22.513	14.894	1.000	1500
b[(Intercept) Patch:3]	-10.372	9.999	-30.103	7.525	1.000	1286
b[(Intercept) Patch:4]	-3.691	9.055	-21.229	16.065	1.000	1277
b[(Intercept) Patch:5]	18.914	11.611	-2.512	39.682	0.999	1286
b[(Intercept) Patch:6]	1.420	9.407	-15.437	23.192	1.001	1494
b[(Intercept) Patch:_NEW_Patch]	0.147	16.769	-35.873	30.254	1.001	1500
sigma	17.794	3.780	11.413	25.219	1.000	1090
Sigma[Patch:(Intercept),(Intercept)]	253.854	281.451	0.002	755.827	0.998	1335
mean_PPD	29.846	5.328	18.819	39.893	0.998	1500
log-posterior	-123.105	3.576	-130.229	-117.184	0.999	945

Table C7: Modelled values of relative holdfast size one year after damage

term	estimate	std.error	conf.low	conf.high	rhat	ess
(Intercept)	1.523	0.169	1.178	1.831	1.000	1478
damageHalf	0.044	0.205	-0.337	0.469	1.003	1500
damageQuarter	-0.128	0.208	-0.512	0.295	1.001	1414
damageControl	0.013	0.229	-0.425	0.487	1.000	1383
b[(Intercept) patch:1]	0.046	0.103	-0.133	0.281	0.999	1500
b[(Intercept) patch:2]	0.012	0.093	-0.171	0.232	0.999	1500
b[(Intercept) patch:3]	0.015	0.090	-0.180	0.206	1.001	1212
b[(Intercept) patch:4]	-0.043	0.107	-0.289	0.153	0.999	1500
b[(Intercept) patch:5]	-0.014	0.106	-0.266	0.179	0.999	1500
b[(Intercept) patch:6]	-0.032	0.115	-0.320	0.153	1.000	1424

b[(Intercept) patch:_NEW_patch]	0.000	0.141	-0.292	0.267	1.002	1313
sigma	0.530	0.055	0.423	0.632	0.999	1500
Sigma[patch:(Intercept),(Intercept)]	0.019	0.035	0.000	0.079	1.001	1359
mean_PPD	1.512	0.103	1.310	1.705	1.000	1500
log-posterior	-60.382	2.842	-66.384	-55.597	0.999	1421

Table C8: Modelled values of thallus height one year after damage to holdfasts

term	estimate	std.error	conf.low	conf.high	rhat	ess
(Intercept)	88.909	19.780	45.041	124.338	0.999	1422
damageHalf	-10.140	16.137	-43.102	18.656	0.999	1500
damageQuarter	-22.573	17.213	-57.814	8.286	1.004	1497
damageControl	-34.293	17.496	-69.372	-0.929	1.001	1500
b[(Intercept) patch:1]	26.001	19.126	-8.662	65.496	0.998	1353
b[(Intercept) patch:2]	14.975	18.830	-17.292	55.576	0.998	1270
b[(Intercept) patch:3]	27.571	19.253	-8.610	63.703	1.000	1320
b[(Intercept) patch:4]	-21.182	20.170	-61.512	15.727	1.001	1498
b[(Intercept) patch:5]	-21.961	22.014	-68.445	16.280	0.999	1414
b[(Intercept) patch:6]	-21.549	21.504	-64.902	18.733	0.998	1412
b[(Intercept) patch:_NEW_patch]	1.814	35.736	-72.577	72.407	0.999	1500
sigma	40.429	4.687	32.112	50.040	1.001	1240
Sigma[patch:(Intercept),(Intercept)]	1295.753	1355.848	0.085	3645.063	1.000	1260
mean_PPD	82.824	8.094	68.060	98.836	1.000	1500
log-posterior	-285.601	3.324	-292.407	-279.961	1.001	1052

Appendix D: Supplemental information for Chapter 5

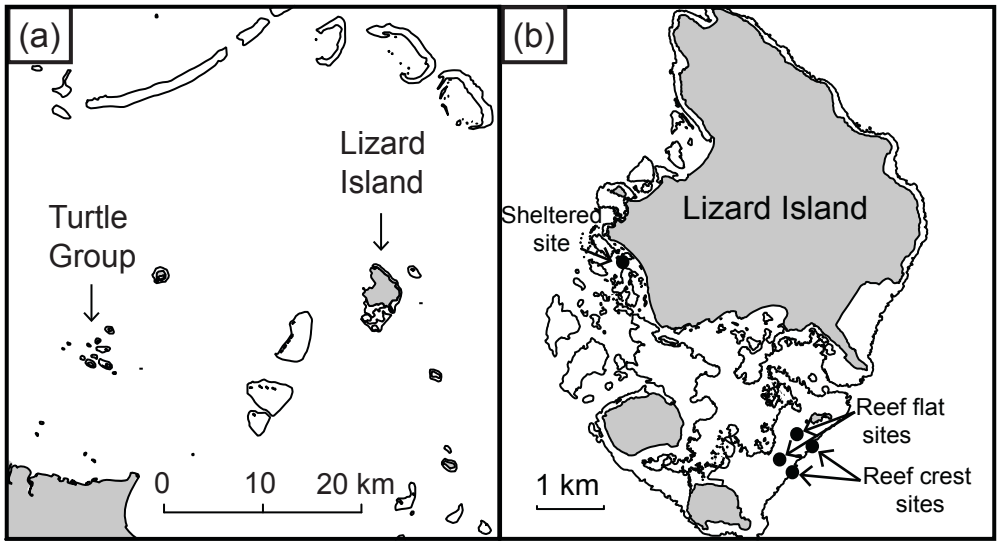

Figure D1: (a) Position of Lizard Island relative to the Turtle Group Islands, the site of adult *Sargassum* collection; (b) map of Lizard Island showing the location of the exposed reef flat and reef crest sites where the tile pairs were deployed, and location of sheltered site where tiles were placed to allow the establishment of EAM assemblages. Modified from Hoey and Bellwood (2009).

Height of turf between EAM with propagules and EAM only tiles

Video stills were taken during the first minute of video footage, and three measurements of turf height were taken from each tile of a pair using the program ImageJ, to determine if there was any difference in turf height between EAM with propagules and EAM only tiles that could have influenced grazing rates.

To examine if the height of turf differed between EAM only and EAM with propagules tiles, a generalised linear model was fitted using the function 'stan_glm', with turf height (mm) as the response variable. Substrate (EAM only or EAM with propagules tile) was included as a fixed factor. The model was fitted with a Gaussian error distribution with an identity link transformation and weakly informative priors on intercept (normal(0,10)) and slope coefficients (normal(0,10)) and error standard

deviation (cauchy(0,5)). Three chains were used, with 4000 iterations, a warmup of 2000 and a thinning factor of three.

The analysis of turf height between EAM only and EAM with propagules tiles revealed that there was no significant difference in the height of turf between the substrate types, with the turf growing on the EAM with propagules tiles averaging a height of 3.77 [3.18, 4.28] mm and the turf on EAM only tiles averaging a height of 4.17 [3.58, 4.74] mm.

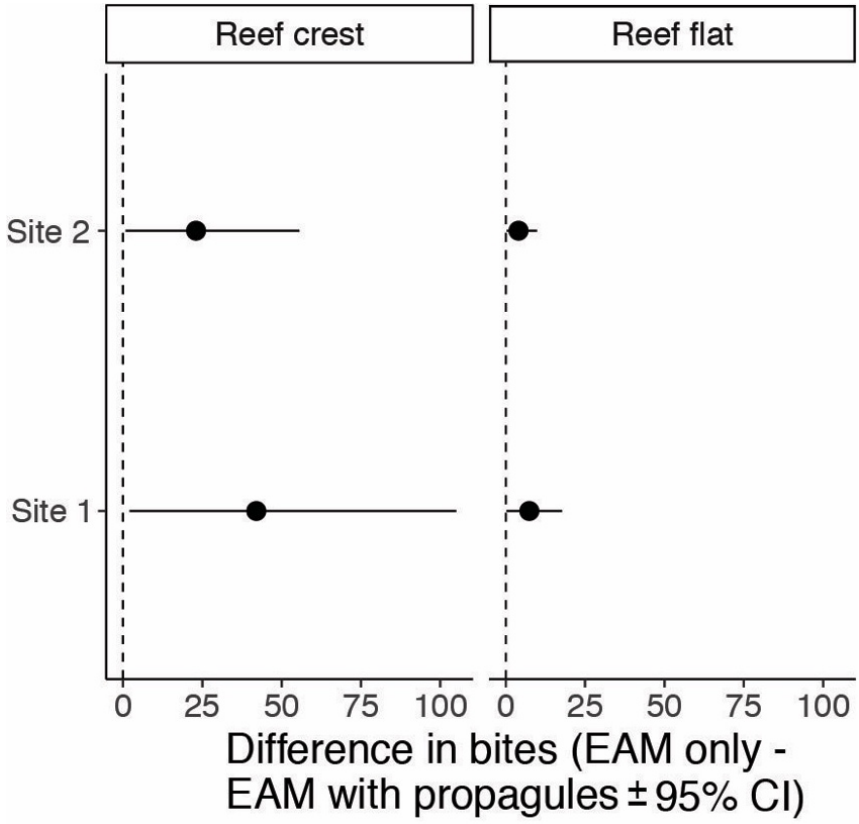

Figure D2: Difference in overall rate of herbivory between EAM only and EAM with propagules tiles in both habitats and sites, using mean ± 95% Credible Intervals

Appendix D

Table D1: List of all fish species that took bites on exposed tiles along with the sum of their bites on EAM only and EAM with propagules over the five days of video. The highest bite count for each species is in bold

Fish species	Sum of bites on EAM with propagules tiles	Sum of bites on EAM only tiles
Acanthurus dussumieri	0	**1**
Acanthurus nigrofuscus	64	**121**
Cirripectes sp.	4	**6**
Ctenochaetus striatus	**213**	195
Dischistodus spp.	2	**12**
Ecsenius aequalis	14	**20**
Ecsenius bicolor	**27**	5
Ecsenius stictus	13966	**18872**
Ecsenius yaeyamaensis	30	**49**
Pomacentrus australis	1	**5**
Pomacentrus chrysurus	78	**167**
Pomacentrus milleri	3	**17**
Pomacentrus moluccensis	2	**21**
Pomacentrus wardi	42	**159**
Salarias alboguttatus	201	**485**
Salarias fasciatus	156	**157**
Scarus flavipectoralis	0	**2**
Scarus schlegeli	411	**629**
Stegastes apicalis	**102**	84
Stegastes nigricans	15	**49**
Zebrasoma scopas	1	**13**

Appendix D

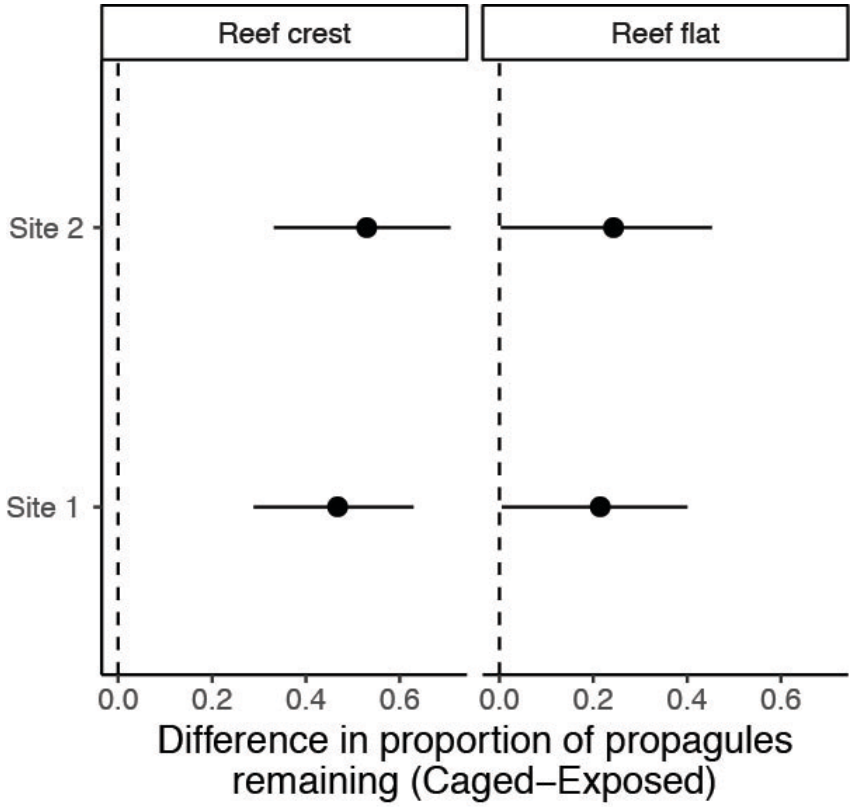

Figure D3: Planned contrasts comparing the difference on proportion of propagules remaining between caged and exposed tiles between reef habitats and sites

Appendix E: Supplemental information for Chapter 6

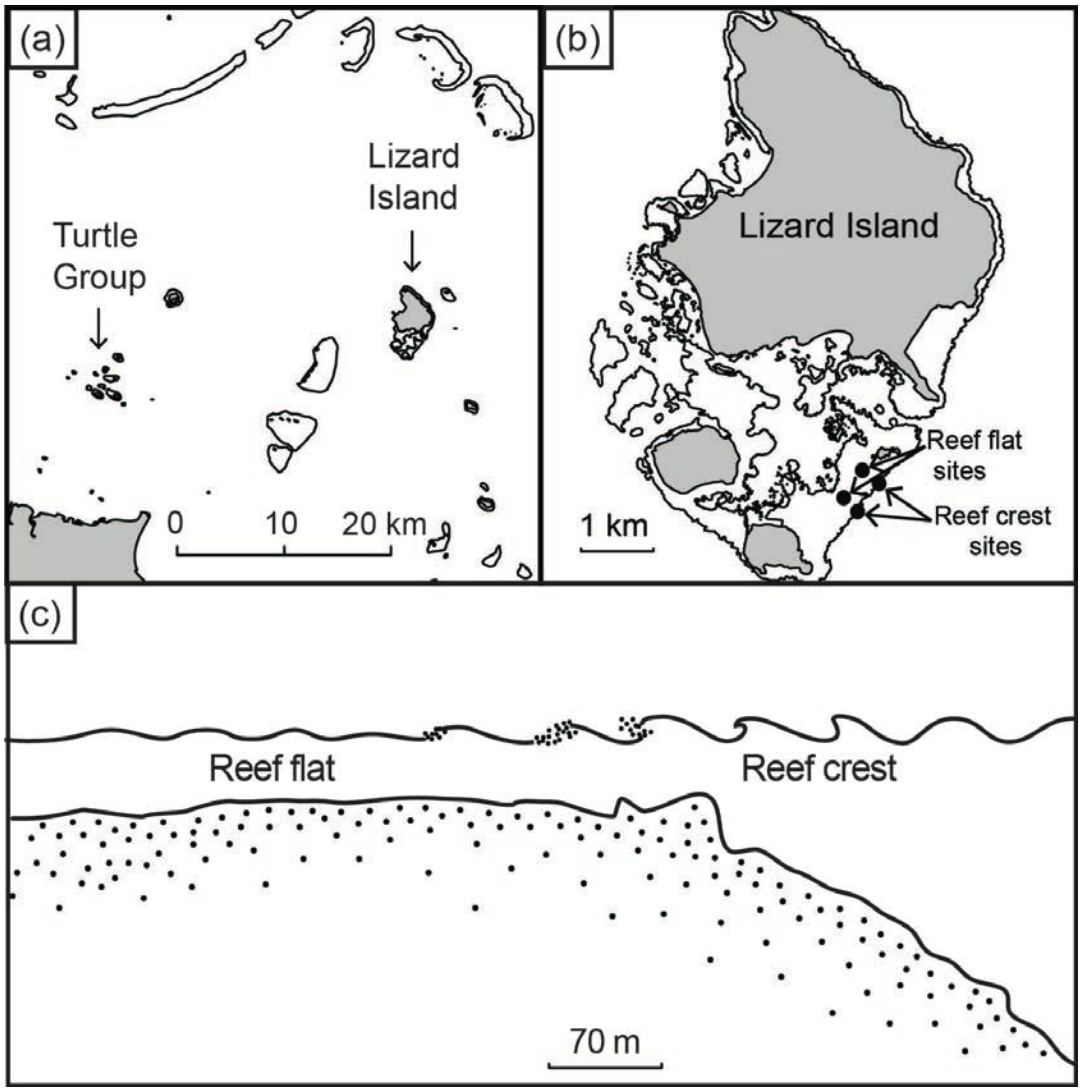

Figure E1: (a) Position of Lizard Island relative to the Turtle Group Islands, the site of adult *Sargassum* collection; (b) map of Lizard Island showing the location of the exposed reef flat and reef crest sites where tiles were deployed; (c) schematic of the reef flat and reef crest habitats. Modified from Hoey and Bellwood (2009).

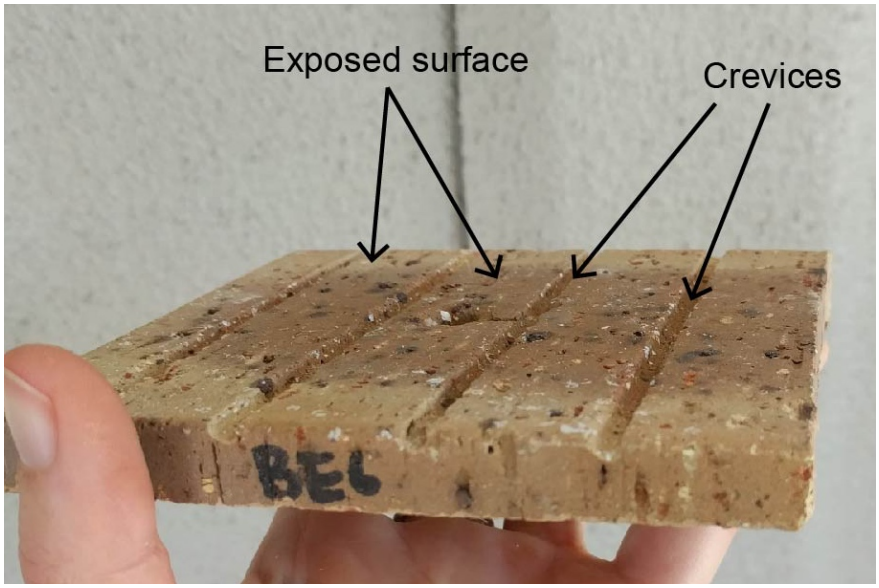

Figure E2: Example of a tile onto which *Sargassum* propagules were settled, showing 3mm-wide crevices and exposed microhabitats.

Fish surveys

The number and diversity of fishes was higher on the reef crest than the reef flat; 48 different species were identified on the reef crest and only 22 on the reef flat (Table 1). The abundance of Ecsenius blennies was almost 9x higher on the reef crest compared to the reef flat, with an average (mean ± SE) of 8.8 ± 2.6 individuals per 50 m^2 on the reef crest compared to 1 ± 0 per 50 m^2 (Table 1). There was an average of 6 ± 1.6 *Ctenochaetus striatus* individuals per 50m^2 on the reef crest and none seen on the reef flat. No *S. fasciatus* individuals were seen on the reef crest, and an average of 1 ± 0 per 50 m^2 was seen on the reef flat.

Table E1: Fish survey results from reef crest and reef flat habitats.

Habitat	Fish species	Average number of fish per 50m transect	SE
Crest	Abudefduf vaigiensis	1.00	NA
Crest	Acanthurus auranticavus	2.67	0.76
Crest	Acanthurus blochii	2.00	0.58
Crest	Acanthurus dussumieri	3.67	0.90

Crest	Acanthurus grammoptilus	2.00	NA
Crest	Acanthurus lineatus	2.67	1.67
Crest	Acanthurus nigrofuscus	8.70	2.28
Crest	Acanthurus olivaceus	3.63	0.73
Crest	Atrosalarias holomelas	1.00	NA
Crest	Chlorurus bleekeri	1.00	NA
Crest	Chlorurus sordidus	2.00	1.00
Crest	Chrysiptera caesifrons	6.33	0.80
Crest	Chrysiptera flavipinnis	2.00	NA
Crest	Chrysiptera rollandi	1.67	0.33
Crest	Cirripectes stigmaticus	1.00	NA
Crest	Crossosalarias macrospilus	1.00	NA
Crest	Ctenochaetus striatus	6.00	1.59
Crest	Ecsenius bicolor	1.00	0.00
Crest	Ecsenius stictus	8.80	2.46
Crest	Eviota guttata	1.00	NA
Crest	Helcogramma chica	2.67	0.88
Crest	Naso annulatus	2.00	0.32
Crest	Naso unicornis	1.20	0.20
Crest	Neoglyphidon melas	1.00	NA
Crest	Plectroglyphidodon dickii	1.50	0.50
Crest	Plectroglyphidodon lacrynatus	7.00	NA
Crest	Pomacentrus adelus	4.00	NA
Crest	Pomacentrus amboinensis	6.00	1.35
Crest	Pomacentrus bankanensis	9.00	1.75
Crest	Pomacentrus chrysurus	6.67	1.91
Crest	Pomacentrus imitator	3.00	1.53
Crest	Pomacentrus nagasakiensis	8.00	1.53
Crest	Pomacentrus wardi	65.33	8.60
Crest	Scarus dimidiatus	1.33	0.33
Crest	Scarus frenatus	1.44	0.24
Crest	Scarus ghobban	2.00	0.58
Crest	Scarus niger	1.00	0.00
Crest	Scarus oviceps	1.50	0.50
Crest	Scarus psittacus	1.20	0.20
Crest	Scarus rivulatus	3.20	1.02
Crest	Scarus schlegeli	1.00	0.00
Crest	Siganus canaliculatus	22.50	7.50
Crest	Siganus corallinus	3.00	1.00
Crest	Siganus doliatus	3.00	0.45
Crest	Siganus puellus	3.00	1.00
Crest	Siganus punctatus	2.00	NA

Crest	Stegastes apicalis	1.33	0.33
Crest	Zebrasoma scopas	2.67	0.88
Crest	Zebrasoma veliferum	1.50	0.50
Flat	Acanthurus dussumieri	5.00	NA
Flat	Acanthurus nigrofuscus	3.67	2.19
Flat	Chlorurus sordidus	5.00	NA
Flat	Chrysiptera caesifrons	1.00	0.00
Flat	Chrysiptera cyanea	1.00	NA
Flat	Dischistodus prosopotaenia	1.00	NA
Flat	Dischitodus pseudochrysopecilus	1.33	0.33
Flat	Ecsenius stictus	1.00	0.00
Flat	Hemiglyphidodon plagiometopon	2.00	NA
Flat	Juv.Parrotfish	3.60	0.93
Flat	Naso annulatus	1.50	0.29
Flat	Naso unicornis	1.00	NA
Flat	Pomacentrus adelus	59.17	11.60
Flat	Pomacentrus amboinensis	7.00	5.00
Flat	Pomacentrus wardi	12.50	4.52
Flat	Salarias fasciatus	1.00	0.00
Flat	Scarus psittacus	1.00	NA
Flat	Scarus rivulatus	2.00	1.00
Flat	Siganus canaliculatus	20.00	NA
Flat	Siganus doliatus	2.00	NA
Flat	Stegastes apicalis	1.00	NA
Flat	Zebrasoma veliferum	1.00	NA

Table E2: Model summary of propagule survival after 5-day deployment at Lizard Island

term	estimate	std.error	conf.low	conf.high	rhat	ess
(Intercept)	0.70	0.07	0.58	0.84	1	1286
SurfaceExposed	-0.02	0.08	-0.17	0.13	0.998	1500
HabitatReef Flat	-0.06	0.10	-0.25	0.14	1	1232
TreatmentUncaged	0.10	0.10	-0.09	0.28	1	1343
SurfaceExposed:HabitatReef Flat	0.11	0.11	-0.10	0.33	0.999	1500
SurfaceExposed:TreatmentUncaged	-0.36	0.11	-0.60	-0.17	0.999	1500
HabitatReef Flat:TreatmentExposed	0.06	0.14	-0.21	0.35	1	1365
SurfaceExposed:HabitatReef Flat:TreatmentUncaged	0.18	0.15	-0.13	0.47	0.998	1500
b[(Intercept) id:BC1]	-0.15	0.11	-0.39	0.05	0.999	1222
b[(Intercept) id:BC10]	-0.05	0.10	-0.25	0.15	0.999	1500
b[(Intercept) id:BC11]	-0.08	0.11	-0.28	0.12	1.002	1500
b[(Intercept) id:BC12]	0.02	0.11	-0.18	0.22	1	1500
b[(Intercept) id:BC2]	-0.08	0.11	-0.29	0.12	1.001	1288
b[(Intercept) id:BC3]	-0.05	0.11	-0.26	0.15	0.998	1500
b[(Intercept) id:BC4]	-0.16	0.11	-0.38	0.04	1.004	1276
b[(Intercept) id:BC5]	0.09	0.11	-0.11	0.30	0.999	1189
b[(Intercept) id:BC6]	0.03	0.11	-0.19	0.23	1	1500
b[(Intercept) id:BC7]	0.30	0.13	0.04	0.55	1.003	1125
b[(Intercept) id:BC8]	-0.11	0.10	-0.32	0.09	0.999	1500
b[(Intercept) id:BC9]	-0.03	0.11	-0.24	0.17	0.999	1489
b[(Intercept) id:BE1]	0.05	0.10	-0.14	0.25	0.999	1500
b[(Intercept) id:BE10]	0.04	0.10	-0.16	0.24	0.999	1500
b[(Intercept) id:BE11]	0.01	0.11	-0.20	0.22	1	1500
b[(Intercept) id:BE12]	-0.08	0.11	-0.28	0.14	1.002	1500
b[(Intercept) id:BE2]	-0.11	0.11	-0.32	0.10	0.999	1470
b[(Intercept) id:BE3]	-0.07	0.11	-0.29	0.12	0.999	1440
b[(Intercept) id:BE4]	-0.09	0.10	-0.29	0.12	1.001	1500
b[(Intercept) id:BE5]	-0.08	0.11	-0.29	0.13	1.001	1415
b[(Intercept) id:BE6]	-0.16	0.11	-0.38	0.05	1	1500
b[(Intercept) id:BE7]	0.03	0.11	-0.17	0.25	0.998	1375
b[(Intercept) id:BE8]	0.00	0.11	-0.20	0.20	1.002	1382
b[(Intercept) id:BE9]	-0.08	0.11	-0.28	0.13	0.999	1500
b[(Intercept) id:SC1]	-0.08	0.10	-0.28	0.12	1	1500
b[(Intercept) id:SC10]	-0.09	0.11	-0.30	0.11	1	1500
b[(Intercept) id:SC11]	0.20	0.12	-0.03	0.42	0.999	1387
b[(Intercept) id:SC12]	-0.13	0.11	-0.35	0.08	1	1500
b[(Intercept) id:SC2]	0.30	0.13	0.06	0.56	0.999	1024
b[(Intercept) id:SC3]	0.08	0.11	-0.12	0.30	1.002	1500
b[(Intercept) id:SC4]	-0.03	0.11	-0.24	0.19	0.999	1493
b[(Intercept) id:SC5]	-0.04	0.11	-0.22	0.20	1	1442
b[(Intercept) id:SC6]	-0.01	0.11	-0.21	0.21	0.998	1452
b[(Intercept) id:SC7]	0.05	0.10	-0.15	0.24	1.001	1500
b[(Intercept) id:SC8]	-0.14	0.11	-0.35	0.07	1	1255

b[(Intercept) id:SC9]	0.07	0.10	-0.13	0.29	1.006	1500
b[(Intercept) id:SE1]	-0.02	0.11	-0.21	0.19	1.001	1500
b[(Intercept) id:SE10]	-0.06	0.11	-0.26	0.15	0.998	1500
b[(Intercept) id:SE11]	-0.07	0.10	-0.26	0.15	1.001	1500
b[(Intercept) id:SE12]	0.03	0.11	-0.18	0.24	1.002	1500
b[(Intercept) id:SE2]	0.01	0.10	-0.20	0.20	0.999	1347
b[(Intercept) id:SE3]	0.09	0.11	-0.11	0.30	1.001	1208
b[(Intercept) id:SE4]	0.10	0.11	-0.11	0.30	1.001	1278
b[(Intercept) id:SE5]	0.20	0.12	-0.03	0.43	0.999	1062
b[(Intercept) id:SE6]	0.15	0.11	-0.08	0.36	0.999	986
b[(Intercept) id:SE7]	0.09	0.11	-0.09	0.33	1.001	1158
b[(Intercept) id:SE8]	-0.01	0.10	-0.22	0.19	1.001	1500
b[(Intercept) id:SE9]	0.09	0.11	-0.11	0.32	0.998	1500
b[(Intercept) id:_NEW_id]	0.00	0.16	-0.30	0.35	1	1500
sigma	0.19	0.02	0.15	0.23	1.004	892
Sigma[id:(Intercept),(Intercept)]	0.02	0.01	0.01	0.05	1.002	1051
mean_PPD	0.69	0.03	0.63	0.74	0.999	1500
log-posterior	-56.62	9.47	-75.33	-38.55	1.006	837

Table E3: Tidy output of the difference in slope estimates for planned contrasts comparing the survival of propagules between habitats and treatments

Habitat	Treatment	estimate	std.error	conf.low	conf.high	Probability of a difference between crevice and top surfaces
Reef Crest	Uncaged	0.378	0.079	0.228	0.531	100 %
Reef Crest	Caged	0.019	0.077	-0.134	0.169	59.6 %
Reef Flat	Uncaged	0.091	0.073	-0.048	0.235	89.4 %
Reef Flat	Caged	-0.086	0.081	-0.257	0.062	85.6 %